ESTIMATING GORILLA ABUNDANCE BY DUNG COUNT IN THE NORTHERN PART OF MOUKALABA-DOUDOU NATIONAL PARK, GABON

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ABSTRACT Nest count is not an appropriate method to estimate abundance of gorillas and chimpanzees where both species live sympatrically. To apply an alternative method that could estimate their abundance separately, we examined dung count for gorillas on line transects. In the northern part of Moukalaba-Doudou National park, Gabon, we conducted a survey of gorilla dung piles (DPs) along the 11 line transects of 44.3 km in total length. First, we counted and marked all encountered dung piles and estimated DP density by the distance sampling method. After two days, we walked the same transects and checked whether the marked DPs were still recognizable, in order to calculate a daily dung disappearance rate. Using DP density, daily dung disappearance rate and the defecation frequency extrapolated from the other western gorilla populations, we calculated the density of gorilla. DP density was estimated at 102.3 dps/km^2. Dung piles of gorillas are easily discriminated from those of chimpanzees, so dung pile density is considered as a good indicator of gorilla abundance. However, individual density derived from DP density, daily dung disappearance rate and defecation rate seemed to be significantly overestimated. Precise information on dung decay duration, age/sex difference in defecation rate, dietary effects on defecation rate, and group-level DP production frequency are needed for a reliable individual density estimate. No significant difference was found in the encounter frequency of dung piles between the home range of our habituated gorilla group and those of adjacent areas, suggesting an overall high density of gorillas in the northern part of the Park.

RÉSUMÉ Le comptage des nids n’est pas une méthode appropriée pour estimer l’abondance des gorilles et des chimpanzés là où les deux espèces vivent en sympatrie. Afin d’appliquer une méthode alternative d’estimation des populations de ces espèces, nous avons compté les excréments des gorilles le long de transects en ligne. Dans la partie nord du Parc National de Moukalaba-Doudou (Gabon), nous avons conduit un recensement des excréments laissés par les gorilles (DPs) le long de 11 transects en ligne pour un total de 44,3 km. Nous avons dénombré et marqué tous(DPs) les excréments et estimé leur densité en utilisant la méthode d’échantillonnage par les distances (Distance Sampling Method). Les lignes de transects ont été parcourues à nouveau deux jours après ce premier recensement et les excréments marqués ont été contrôlés afin de calculer un ratio-jour de disparition des excréments. A partir de la densité d’excréments, du ratio-jour de leur disparition et de la fréquence des défécations des gorilles estimée auprès des autres populations de gorilles de l’ouest, nous avons calculé la densité de gorilles du PNMB. Le nombre d’individus au km^2 ainsi estimé est de 102,3. Les excréments de gorilles sont facilement identifiables et distinguables de ceux des chimpanzés. L’estimation de leur densité est donc considérée comme un bonne indicateur de l’abondance des cette espèce dans le milieu. Cependant, la densité des gorilles étant calculée à partir de celles des excréments, de leur taux de disparition journalier et de la fréquence des défécations, nous pensons que cette densité est surestimée. Des informations précises sur le désagrègement des excréments et sur les fréquences de défécation des animaux en fonction de l'âge et du sexe ainsi que sur les effets des différents aliments ingérés sur cette fréquence (comme la production d'excrément au niveau du groupe) sont nécessaire pour calculer avec plus de précision la densité des gorilles. Par ailleurs, nous n'avons pas trouvé de différence entre la fréquence de rencontres des excréments dans l'habitat de notre groupe d'étude avec celle des habitats des groupes adjacents. Cette absence de différence suggère une forte densité de gorilles dans toute la partie nord du PNMB.

Key Words: Density estimate; Dung piles (DPs); Defecation rate; Gorilla; Moukalaba-Doudou; Conservation.

INTRODUCTION

Great ape populations have been rapidly disappearing from their natural habitats in Central Africa. Major threats to their survival include hunting for the bushmeat trade, habitat loss and fragmentation caused by logging and mining, and epidemics of infectious diseases such as Ebola hemorrhagic fever constitute major threats to their survival (Harcourt 1996, 2003; Plumptre *et al.*, 2003; Tutin, 2002; Walsh *et al.*, 2003; Leroy *et al.*, 2004). In order to design and carry out effective measures for gorilla conservation, it is essential to determine their current distribution and abundance. However, very little information is available on their abundance, particularly for western lowland gorillas, due to the methodological difficulties of their density estimates.

The previous estimates of ape densities in lowland tropical forests of Africa have been largely based on nest counts (Carroll, 1988; Fay, 1989; Blake *et al.*, 1995; Yamagiwa *et al.,* 1995; Furuichi *et al.*, 1997; Furuichi *et al.*, 2001; Blom *et al.*, 2001, 2004; Huijbregts *et al.*, 2003; Sanz *et al.*, 2006; Morgan, 2007; Morgan *et al.*, 2006; Arnhem *et al.*, 2008). Data on nest production and nest decay rate were used for calculation of ape density (Tutin & Fernandez, 1984). However, these rates vary depending on a number of conditions. A single gorilla occasionally builds two or more nests, and they frequently sleep on bare ground without a visible nest (Remis, 1993; Tutin *et al.*, 1995; Mehlman & Doran, 2002). Nest decay rate varies with seasons or vegetation types, and these variations may produce inaccurate estimates of gorilla abundance (Walsh & White, 1999). It is also difficult to distinguish gorilla nests from those of chimpanzees in the areas that gorillas and chimpanzees inhabit sympatrically (Sanz *et al.*, 2006). Gorillas frequently build nests in trees as do chimpanzees, and only well trained researchers and trackers can distinguish nest builders confidently at fresh nest sites (Blom *et al.*, 2004). Although several parameters have been established based on the differences in nest construction between gorillas and chimpanzees such as nest height and size, the reliability of such criteria is still uncertain (Furuichi *et al.,* 1997; Sanz *et al.*, 2006).

Therefore, we focus on dung as another useful index of gorilla density. Dung has been used as an effective useful method to estimate the abundance of mammals such as ungulates, elephants and other herbivores in tropical Africa (Merz, 1986; Fuller, 1991; Plumptre & Harris, 1995; Walsh & White, 1999; Barnes, 2001; Morgan, 2007). Dung piles of gorillas and chimpanzees are easily distinguishable. Gorillas defecate more frequently than they build nests, and their dung piles decay faster than nests. Dung count could be useful for accurate estimates of gorilla density if their defecation rate and dung decay rate were available. Schaller (1963) reported that mountain gorillas defecated 5.5 times a day in the Virungas, and Tutin *et al.* (1991) estimated 4 to 5 times a day for western lowland gorillas at Lopé. Defecation rate may vary with rainfall, diet, age, and health conditions (White & Edwards, 2000), but we can use these established decay rates for estimates of gorillas density.

The purpose of this study is to evaluate the applicability of dung counts for estimates of gorilla abundance. We conducted dung count by line transect in the northern part of Moukalaba-Doudou National Park, Gabon. We estimated dung decay rate and overall dung pile density in the study area. Based on these estimates, we tried to calculate individual gorilla density and compared dung encounter rate between the home range of our focal study group and those of other regions. We also point out the advantages of using dung count and this method's problems that remain to be solved.

METHODS

I. Study Site

Field study was conducted in the Moukalaba-Doudou National Park, Gabon (Fig. 1). The Park covers an area of 5,028 km^2, which consists of a mosaic of forest, savanna, and swamp. The Park faces to the Atlantic Ocean on its southwestern boundary. The Doudou Mountain Range runs north and south at altitudes up to 900 m. The vegetation is a complex mosaic of semi-primary forest, secondary forest, *Musanga cecropioides* dominated forest, savanna and swamp (Iwata & Ando, 2007). Savanna dominates in the southern area, and the proportion of forests areas increases going north. The study area is the northern part of the Park.

Annual rainfall in the study area fluctuated from 1,582 mm to 1,886 mm for three years (2004–2006). Mean monthly minimum and maximum temperature ranged from 21.3 to 24.1°C, and 29.3 to 33.7°C, respectively. There are two distinct seasons, a rainy season from October to April and a dry season from May to September. During the three months in the middle of the dry season, it seldom rains. People report a short dry season around December-January, but this is not always distinct.

II. Line Transect Census

We employed a systematic count of dung piles from line transects as the method to estimate the density of gorillas. The census was conducted from September to October 2002.

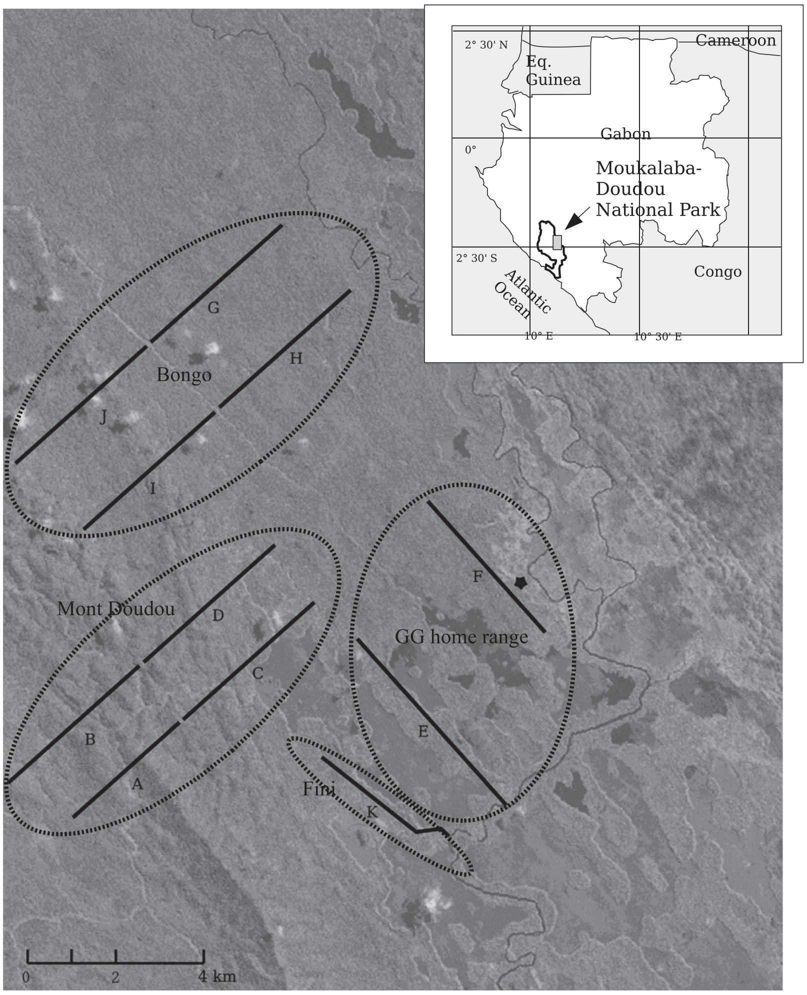

Fig. 1. Study site and line transects (solid line). Dashed circles indicate subregions (see text). Black star indicates camp site.

Eleven transect lines were cut in seven zones in the northern part of the park (Fig. 1, Table 1). The length of each transect line was four kilometers, except for A (3 km) and E (5.3 km). Total length of the transects was thus 44.3 km.

We classified the transects into four subregions, GG home range, Mont Doudou, Bongo, and Fini (Table 1, Fig. 1). GG home range is the home range of the focal gorilla group (Group Gentil) of our research project (See Ando *et al.* (2008) for the detail of this group). Mont Doudou is situated in the mountainous area, Bongo is the area of mixed lowland forest north to GG home range, and Fini is located in the riverine area south of the GG home range.

During the census, each of the authors walked on the transects at a rate of 0.5–1.0 km/h with two local field assistants while detecting dung piles of gorillas. When a gorilla dung pile was found, the spot was marked and the perpendicular

Table 1. List of line transects and number of dung piles.

Subregion	Transect ID	Length (km)	Number of dung piles	Forest type
Mont Doudou	A	3	6	Semi-montane
	B	4	3	Semi-montane
	C	4	0	Semi-montane, mixed-species, riverine
	D	4	3	Semi-montane, mixed-species
GG home range	E	5.3	2	mixed-species, riverine
	F	4	6	mixed-species, secondary, Musanga-dominated-secondary
Bongo	G	4	4	mixed-species
	H	4	3	mixed-species
	I	4	5	mixed-species, semi-montane
	J	4	10	mixed-species, semi-montane
Fini	K	4	6	riverine, mixed-species
Total		44.3	48	

distance from the center of the transect line to the center of the dung pile was recorded. Distance was recorded in 1-meter segments; when the distance of a dung pile from the transect line was less than 50 cm, it was recorded as 0 m, 0.5–1.5 m as 1 m, and so on. When fragments of dung of apparently different ages were found at the same place, they were regarded as different dung piles. We defined three age classes from the measurement of dung diameter: under 40 mm, Juvenile; 40–60 mm, adult female or blackback male; over 60 mm, silverback male. When a nest group was detected, we checked around the nest group for dung piles. Fragments of dung detected around a nest site were regarded as a single dung pile because they were detected by a single detection effort.

III. Dung Pile Density

Density of dung piles were estimated by the distance sampling method (Ross & Reeve, 2001; Backland *et al.*, 1993). We applied the following equation:

$$\text{Dung pile density} = n/2wLP \qquad \text{(Eq. 1)}$$

where n indicates the number of dung piles detected, w indicates detection distance, L indicates the length of transect, and P indicates the probability of detecting a dung pile that lie within distance w from the transect (Backland *et al.*, 2001, Walsh & White, 1999) We used PROGRAM DISTANCE 5.0 (Thomas *et al.*, 2006) for calculation of the dung pile density estimate.

IV. Gorilla Individual Density

Provided the dung pile density (D_{dp}), gorilla individual density is calculated with two additional parameters, daily dung disappearance rate (R_{dd}, the proportion of dung piles that disappear each day) and individual defecation frequency (F_d).

First, in order to estimate dung decay rate, we walked each transect two days after the census to verify whether marked dung pile were still recognizable.

We employed two assumptions: (1) Individual gorilla density does not change within a few days; (2) Under the assumption 1, the existing set of dung piles in the study area does not change. In other words, the number of dung piles that disappear within a few days is equal to those newly deposited.

Employing these assumptions, the daily dung disappearance rate from the existing set of dung piles is equal to the rate of dung piles added to the existing set in a day. Accordingly, dung pile density per day is obtained as follows:

$$\text{dung pile density per day} = D_{dp} \times R_{dd}$$

Daily dung disappearance rate can be estimated by assuming that dung disappears at a constant instantaneous rate r, so N_t, the number of dung piles at time t is obtained as follows:

$$N_t = N_0 \exp(rt)$$

where r is a negative constant and N_0 is the number of dung piles at time 0. Rearranging gives us an instantaneous decay rate of

$$r = \ln(N_t/N_0)/t$$

The daily disappearance rate is then obtained as follows:

$$R_{dd} = 1 - \exp(r)$$

Consequently, the individual density of gorillas is obtained as follows:

$$\text{Gorilla density} = D_{dp} \times R_{dd}/F_d \qquad \text{(Eq. 2)}$$

Because defecation rate, i.e. the number of times of defecation per day per individual, was not available at the moment for the Moukalaba gorillas, we extrapolated the previous estimates of the defecation rate of Lopé gorillas, i.e. 4–5 times per day (Tutin *et al.*, 1991; White & Edwards, 2000).

RESULTS

I. Dung Pile Density

A total of 48 dung piles were encountered during the census. The number of dung piles counted in each transects is shown in Table 1.

Perpendicular distances of dung piles from the transect line are shown in Fig. 2. Most of the dung piles were detected within 2 m from the transect line, while several dung piles, especially those accompanied by nests, were detected at a

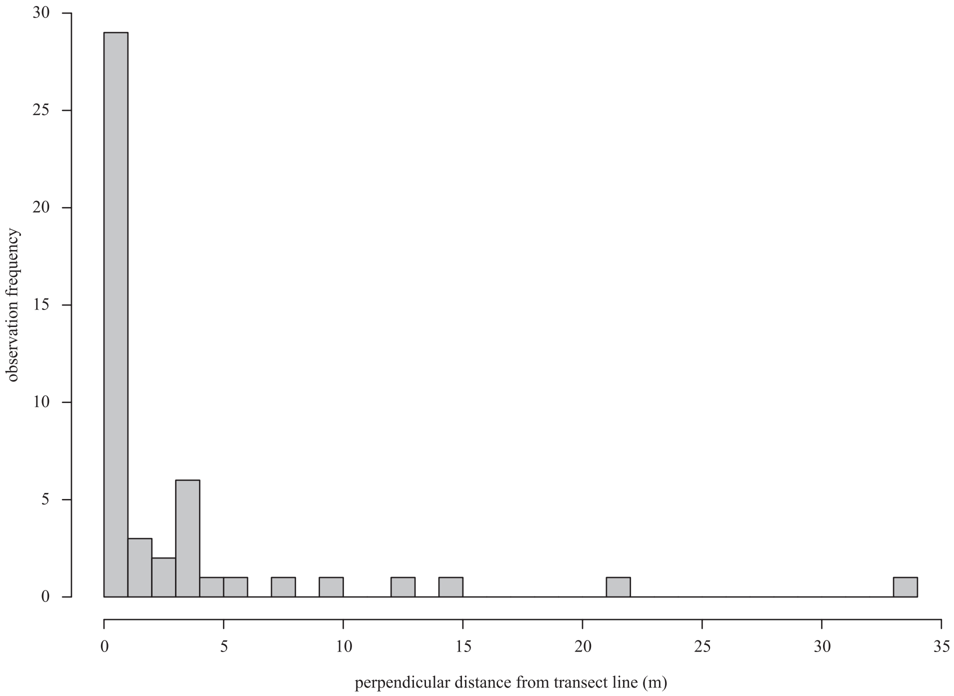

Fig. 2. Frequency distribution of perpendicular distances of dung piles from transect line.

Table 2. Number of dung piles for each zone

Subregion	Mont Doudou	GG home range	Bongo	Fini	Total
N. of dung piles	12	8	22	6	48
Transect length (km)	15	9.3	16	4	44.3
DPs/km	0.8	0.86	1.375	1.5	1.08
N. of DPs (expected)	16.25	10.07	17.34	4.33	48

greater distance.

Because the number of dung piles counted at each transect was not large enough to estimate the dung pile density of each transect area, we regarded all of the transects as a single survey unit representing the northern part of the Moukalaba-Doudou National Park. Consequently, dung pile density was estimated at 102.3 piles/km^2, with lower and upper confidence limits of 91.377 and 114.566, respectively. In the analysis, we eliminated the 5% of dung piles at the farthest distance. The detection probability function applied is half-normal with cosine series expansion: the AIC is 197.28.

II. Daily Dung Disappearance Rate and Gorilla Individual Density

Twenty-three dung piles were recognized two days after the census. Accordingly, R_{dd} is calculated as follows:

$$R_{dd}=1-\exp\ (\ln\ (23/48)/2)=0.3077$$

Finally, we obtained the gorilla density following Eq. 2:

$$102.3\times0.3077/4.5=6.99\ \text{gorillas/km}^2.$$

However, we need to be cautious about this value. This problem will be discussed in detail later.

III. Comparison of Dung Encounter Rate Between Areas

The number of dung piles counted and the subtotal transect length of each subregion is shown in Table 2. No significant difference in the dung encounter rate between subregions was detected (χ^2 goodness of fit test, χ^2=3.4537, df=3, p=0.3292).

DISCUSSION

I. Dung Count as an Alternative Measure for Gorilla Abundance

Our study suggests that the dung count may be an effective method to estimate the abundance of gorillas independently from chimpanzees in areas where gorillas and chimpanzees live sympatrically. We can obtain an accurate figure with less sampling effort than that required for nest counts. Although our results for dung pile density had a wide confidence interval, this can be compressed by using a longer transect length to obtain a larger sample size and thus a more reliable estimate.

Due to the shorter duration of dung decay (generally a few days) than that of nest decay (several months), dung pile density represents the abundance of gorillas in the study area during a short period. This may enable us to estimate the temporal abundance of gorillas that can change with their movements. Dung count is expected to be a useful measure to monitor weekly or monthly movements of gorillas and to assess the effects on their movements of environmental changes, such as food availability, the presence of other groups, predation, and human disturbance.

However, there are several problems in getting accurate figures of individual density from dung piles. First, the number of dung piles may not closely represent the number of defecations. It is difficult to observe the defecation event of unhabituated gorillas in natural habitats. A cluster of dung piles detected by a single detection effort during our census may not always match a dung pile deposited by an individual gorilla at one time. This is clear for dung piles detected at a nest site, but it is possible that some of the dung piles visually detected near transects are combinations of dung defecated by plural individuals simultaneously, since gorillas forage in groups with more or less synchronized activities. One logical solution to this problem is to investigate the group level defecation frequency. Once “a cluster of dung piles” are appropriately defined, it is possible to obtain group-level defecation frequency by tracking habituated groups.

However, group-level defecation rate apparently depends on group size and composition. Therefore it is impossible to apply a group-level defecation frequency of a certain group to all of the other groups in the study area. A statistical model of group-level defecation rate and group size and composition should be measured before making assumptions about group/individual density.

Second, the rate of defecation varies with dietary composition. Folivory, especially consumption of fiber, may increase gut passage rates and defecation rates (Milton, 1999). Effects of diet on their defecation rates may also appear in seasonal variations. Western lowland gorillas show distinct variations in diet across habitats (Tutin *et al.*, 1991; Kuroda *et al*., 1996; Remis, 1997a). Increased frugivory and arboreal feeding may decrease defecation rates and thus detection rates of their dung on the ground. Third, defecation of gorillas occurs at a particular time of day. They usually defecate in the early morning and just after the midday rest. These diurnal variations may lead to some biases in estimating their defecation rate. We should take these variations into account for estimates of accurate gorilla abundance.

Dung count is not an appropriate measure to estimate the abundance of chimpanzees. During our census, we did not find dung piles of chimpanzees at any transect, probably due to their faster decay rates and their arboreal defecation. With less fibrous remains (Tutin *et al.*, 1991; Kuroda *et al.*, 1996), chimpanzee dung piles more easily decay than do those of gorillas. The majority of chimpanzee dung may completely decay within a few hours after defecation. As chimpanzees exhibit more arboreal habits than gorillas, they often defecate from up in a tree. Such dung is scattered into tiny fragments before it reaches the ground, which is difficult to find from a distance.

Our study suggests that dung pile density is a good index of gorilla abundance where gorillas and chimpanzees live sympatrically, but it is not a good measure for estimating the abundance of sympatric chimpanzees, and the method needs additional information to get a precise number of individual gorillas.

II. Abundance of Gorillas in the Moukalaba-Doudou National Park

We calculated a high density of gorillas (6.99 gorillas/km^2) in our study site. This is the second highest density among habitats of western lowland gorillas (Sarmiento, 2003; Morgan, 2007; Arnhem *et al.*, 2008, Morgan *et al.* 2006; Blom *et al.*, 2004). Our results may possibly overestimate their actual density. A semi-habituated group (GG) constitutes of 22 individuals (a silverback male, a blackback male, 11 females and 9 immatures) ranged 12.4 km^2 in our study site annually (Ando *et al.*, 2008). The GG home range is partly overlapping with two or three neighboring groups and at least two solitary males. Assuming that range overlap of neighboring groups is about half of their range, and that the average group size is about 10 individuals as estimated in many habitats of western lowland gorillas (Magliocca *et al.,* 1999; Gatti *et al.,* 2004; Parnel, 2002), individual density in the GG home range is about 3 gorillas/km^2. Our estimate is about twice higher than this reliable estimate.

Although our overestimation was caused by various reasons, we possibly underestimate the rate of dung production due to the period of our census. Gorillas increased fruit eating in September and October. Strong frugivory increases the daily path length of western lowland gorillas (Tutin, 1996; Remis, 1997b; Goldsmith, 1999). Frugivory also increases reuse of the previous nest sites by gorillas at Moukalaba (Iwata & Ando, 2007). These tendencies may have increased the appearance of gorillas on the transects and thereby increased the density of dung piles during our census period.

The home range of GG is partly dominated by *Musanga cecropioides* and gorillas heavily depend on the fruit of this species from July to September when other kinds of fruit are scarce (Takenoshita, 2004). These observations suggest that *Musanga* fruits provides an important food source to support the high density of gorillas in our study area. However, the results of our census showed no difference in dung encounter rates between the home range of GG and other subregions in our study area. Gorillas are possibly distributed at high density from mountains to lowland and close to human settlements throughout the study area. Although the majority of plant species tend to bear fruits in peak during the rainy season, several species such as *Cissus dinklagei* and *Klainedoxa gabonensis* have long fruiting periods and are constantly available regardless of the season (Takenoshita *et al*., 2008). The constant fruit supply might be the key factor supporting the overall high density of gorillas in our study area.

III. Applicability of Dung Count and Nest Count to Density Estimates of Gorillas

Both dung count and nest count have advantages and disadvantages as an indicator of great ape abundance (Table 3). Although it is difficult to find the individual density, dung count is a conventional, easy-to-conduct survey method for gorilla abundance. Conservation of the great apes in central Africa is an expensive operation, and financial support is not sufficient (Wilkie *et al*., 2001; Blom, 2004). Therefore, a low cost, conventional way to monitor the population dynamics of an area is useful. The problem is that dung count is not applicable for determining chimpanzee abundance, but in combination with marked nest census without detailed investigation of nest characteristics for builder discrimination, one can get an indicator of chimpanzee abundance as the ratio of great ape nest density and gorilla dung pile density.

The advantage of nest count is that with detailed investigation of nest

Table 3. Comparison of dung count and nest count.

	Dung count	Nest count
discrimination between gorillas' and chimpanzees'	easy	need statistical model*
variance of decay duration	small	large, but can be standardized by marked nest census**
estimation of creation frequency	nearly impossible	close to 1/day

* Sanz *et al*. (2006)
** Furuichi *et al*. (2001); Plumptre & Reynolds (1996)

characteristics that enable precise discrimination of nest builders, one can achieve a reliable estimate of individual density of gorillas and chimpanzees in areas of interest (Sanz *et al.*, 2006). However, as mentioned above, in order to apply a model for discrimination to different habitats and to different periods in the same habitat, researchers must repeat the measurement of parameters needed in the model at each time. This requires hard work.

Researchers can use both dung and nest count methods according to the purpose of their census. When reliable information on the present number of great ape individuals is required, they may apply a marked nest census while considering the parameters needed for a function that can discriminate nest builders. This may be effective for making an assessment of population density in the candidate protected area. On the other hand, when getting an exact number of individuals is less important than economizing on survey effort, dung count may be a satisfactory approach. Monthly monitoring of existing protected areas would be a suitable trial case. In order to get reliable information on gorilla abundance in all of their habitats and to construct effective measures for their conservation, these two census methods should be combined appropriately.

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REFERENCES

Ando, C., Y. Iwata & J. Yamagiwa 2008. Progress of habituation of western lowland gorillas and their reaction to observers in Moukalaba-Doudou National Park, Gabon. *African Study Monographs Supplementary Issue*, 39: 55–69.

Arnhem, E., J. Dupain, R. Vercauteren-Drubbel, C. Devos & M. Vercauteren 2008. Selective logging, habitat quality and home range use by sympatric gorillas and chimpanzees: A case study from an active logging concession in southeast Cameroon. *Folia Primatologica*, 79: 1-14.

Backland, S.T., D.R. Anderson, K.P. Burnham & J.I. Laake 1993. *Distance Sampling: Estimating Abundance of Biological Populations.* Chapman & Hall, London.

Barnes, R.F.W. 2001. How reliable are dung counts for estimating elephant numbers? *African*

Journal of Ecology, 39: 1-9.

Blake, S., E.Rogers, M.J. Fay, M. Ngangoue & G. Ebeke 1995. Swamp gorillas in northern Congo. *African Journal of Ecology*, 33: 285-290.

Blom, A. 2004. An estimate of the costs of an effective system of protected areas in the Niger Delta Congo Basin Forest Region. *Biodiversity and Conservation*, 13: 2661-2678.

Blom, A., A. Almasi, I.M.A. Heitkonig, J. Kpanou & H.H.T. Prins 2001. A survey of the apes in the Dzanga-Ndoki National Park, Central African Republic: A comparison between the census and survey methods of estimating the gorilla (*Gorilla gorilla gorilla*) and chimpanzee (*Pan troglodytes*) nest group density. *African Journal of Ecology*, 39: 98-105.

Blom, A., R. van Zalinge, E. Mbea, I.M.A. Heitkonig & H.H.T. Prins 2004. Human impact on wildlife populations within a protected Central African forest. *African Journal of Ecology*, 42: 23-31.

Carroll, R.W. 1988. Relative density, range extension, and conservation potential of the lowland gorilla (*Gorilla gorilla gorilla*) in the Dzanga-Sangha region of southwestern Central African Republic. *Mammalia*, 52: 309-323.

Fay, J.M. 1989. Partial completion of a census of the western lowland gorilla (*Gorilla g. gorilla* (Savage and Wyman)) in southwestern Central African Republic. *Mammalia*, 53: 203-216.

Fuller, T.K. 1991. Do pellet count index white-tailed deer numbers and population change? *Journal of Wildlife Management*, 55: 393-396.

Furuichi, T., C. Hashimoto & Y. Tashiro 2001. Extended application of a marked-nest census method to examine seasonal changes in habitat use by chimpanzees. *International Journal of Primatology*, 22: 913-928.

Furuichi, T., H. Inagaki & S. Angoue-Ovono 1997. Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: Employing a new method to distinguish between nests of the two species. *International Journal of Primatology*, 18: 1029-1046.

Gatti, S., F. Levréro, N. Ménard & A. Gautier-Hion 2004. Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoué, Republic of Congo. *American Journal of Primatology*, 63: 111-123.

Goldsmith, M.L. 1999. Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *International Journal of Primatology*, 20: 1-23.

Harcourt, A.H. 1996. Is the gorilla a threatened species? How should we judge? *Biological Conservation*, 75: 165-176.

——— 2003. An introductory perspective: Gorilla conservation. In (A.B. Taylor & M.L. Goldsmith, eds.) *Gorilla Biology*, pp. 407-413. Cambridge University Press, Cambridge.

Huijbregts, B., P. de Wachter, L.S.N. Obiang & M.E. Akou 2003. Ebola and the decline of gorilla *Gorilla gorilla* and chimpanzee *Pan troglodytes* populations in Minkebe Forest, northeastern Gabon. *Oryx*, 37: 437-443.

Iwata, Y. & C. Ando 2007. Nest and nest-site reuse by western lowland gorillas (*Gorilla g. gorilla*) in Moukalaba-Doudou National Park, Gabon. *Primates*, 48: 77-80.

Kuroda, S., T. Nishihara, S. Suzuki & R.A. Oko 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In (W. McGrew, L. Marchant & T. Nishida, eds.) *Great Ape Societies*, pp 71-81. Cambridge University Press, Cambridge.

Leroy, E.M., P. Rouquet, P. Formenty, S. Souquière, A. Kilbourne, J, Froment, M. Bermejo, S. Smit, W. Karesh, R. Swanepoel, S.R. Zaki & P.E. Rollin 2004. Multiple ebola virus transmission events and rapid decline of central african wildlife. *Science*, 303: 387-390.

Magliocca, F., S. Querouil & A. Gautier-Hion 1999. Population structure and group composition of western lowland gorillas in North-Western Republic of Congo. *American Journal of Primatology*, 48: 1-14.

Mehlman, P.T. & D.M. Doran 2002. Influencing western gorilla nest construction at Mondika Research Center. *International Journal of Primatology*, 23: 1257-1285.

Merz, G. 1986. Counting elephants (*Loxodonta Africana cyclotis*) in tropical rain forests with particular reference to Taï National Park, Ivory Coast. *African Journal of Ecology*, 24: 61-68.

Milton, K.A. 1999. A hypothesis to explain the role of meat-eating in human evolution. *Evolutionary Anthropology*, 8: 11-20.

Morgan, B.J. 2007. Group size, density and biomass of large mammals in the Reserve de Faune du Petit Loango, Gabon. *African Journal of Ecology*, 45: 508-518.

Morgan, D., C. Sanz, J.R. Onononga & S. Strindberg 2006. Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. *International Journal of Primatology*, 27: 147-179.

Parnell, R.J. 2002. Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *American Journal of Primatology*, 56: 193-206.

Plumptre, A.J. & S. Harris 1995. Estimating the biomass of large mammalian herbivores in a tropical montane forest: a method of faecal counting that avoids assuming a 'steady state' system. *Journal of Applied Ecology*, 32: 111-122.

Plumptre, A.J. & V. Reynolds 1996. Censusing chimpanzees in the Budongo Forest, Uganda. *International Journal of Primatology*, 17: 85-99.

Plumptre, A.J., A. McNeilage, J.S. Hall & E.A. Williamson 2003. The current status of gorillas and threats to their existence at the beginning of a new millennium. In (A.B. Taylor & M.L. Goldsmith, eds.) *Gorilla Biology*, pp. 414-431. Cambridge University Press, Cambridge.

Remis, M.J. 1993. Nesting behavior of lowland gorillas in the Dzanga-Sanga Reserve, Central African Republic: Implications for population estimates and understandings of group dynamics. *Tropics*, 294: 245-255.

——— 1997a. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *American Journal of Primatology*, 43: 87-109.

——— 1997b. Ranging and grouping patterns of a western lowland gorilla group at Bai Hokou, Central African Republic. *American Journal of Primatology*, 43: 111-133.

Ross, C. & N. Reeve 2001. Survey and census methods: Population distribution and density. In (J.M. Setchell & D.J. Curtis, eds) *Field and Laboratory Methods in Primatology*, pp. 90-109. Cambridge University Press, Cambridge.

Sanz, C., D. Morgan, S. Strindberg & J.R. Onononga 2006. Distinguishing between the nests of sympatric chimpanzees and gorillas. *Journal of Applied Ecology*, 44: 263-272.

Sarmiento, E.E. 2003. Distribution, taxonomy, genetics, ecology, and causal links of gorilla survival: The need to develop practical knowledge for gorilla conservation. In (A.B. Taylor & M.L. Goldsmith, eds.) *Gorilla Biology*, pp. 432-471. Cambridge University Press, Cambridge.

Schaller, G.B. 1963. *The Mountain Gorilla: Ecology and Behavior.* University of Chicago Press, Chicago.

Takenoshita, Y. 2004. Ranging and diet of sympatric chimpanzees and gorillas in the Moukalaba-Doudou National Park, Gabon. *Folia Primatoogica*, 75(S1): 178-179.

Takenoshita, Y., C. Ando, Y. Iwata & J. Yamagiwa 2008. Fruit phenology of the great ape habitat in the Moukalaba-Doudou National Park, Gabon. *African Study Monographs Supplementary Issue*, 39: 23-29.

Thomas, L., J.L. Laake, S. Strindberg, F.F.C. Marques, S.T. Buckland, D.L. Borchers, D.R. Anderson, K.P. Burnham, S.L. Hedley, J.H. Pollard, J.R.B. Bishop & T.A. Marques 2006. *Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment*, University of St. Andrews, UK. Online. http: //www.ruwpa.st-and.ac.uk/distance/ (Accessed December

26, 2007).

Tutin, C.E.G. 1996. Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon. In (W. McGrew, L. Marchant & T. Nishida, eds.) *Great Ape Societies*, pp 58-70. Cambridge University Press, Cambridge.

——— 2002 Saving the gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) of the Congo Basin. *Reproduction, Fertility and Development*, 13: 469-476.

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

Tutin, C.E.G., M. Fernandez, M.E. Rogers, E.A. Williamson & W.C. McGrew 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Philosophical Transactions of The Royal Society of London Series B*, 334: 179-186.

Tutin, C.E.G., Parnell, R.J., White, L.J.T. & M. Fernandez 1995. Nest building by lowland gorillas in the Lopé Reserve, Gabon: Environmental Influences and implications for censusing. *International Journal of Primatology*, 16: 53-76.

Walsh, P.D., K.A. Abernethy, M. Bermejo, R. Beyers, P. De Wachter, M.E. Akou, B. Huijbregts, D.I. Mambounga, A.K. Toham, A.M. Kilbourn, S.A. Lahm, S. Latour, F. Maisels, C. Mbina, Y. Mihindou, S.N. Obiang, E.N. Effa, M.P. Starkey, P. Teffer, M. Thibault, C.E.G. Tutin, L.J.T. White & D.S. Wilkie 2003. Catastrophic ape decline in western equatorial Africa. *Nature*, 422: 611-614.

Walsh, P.D. & L.J.T. White 1999. What it will take to monitor forest elephant populations. *Conservation Biology*, 13: 1194-1202.

White, L.J.T. & A. Edwards 2000. *Conservation Research in the African Rain Forest: A Technical Handbook*. Wildlife Conservation Society, New York.

Wilkie, D.S., J.F. Carpenter & O. Zhang 2001. The under-financing of protected areas in the Congo Basin: So many parks and so little willingness-to-pay. *Biodiversity and Conservation*, 10: 691-709.

Yamagiwa, J., S. Angoue-Ovono & R. Kasisi 1995. Densities of apes' food trees and primates in the Petit Loango Researve, Gabon. *African Study Monographs*, 16: 181-193.

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