Ecological Applications, 17(8), 2007, pp. 2403–2414

MANIPULATING DECAY TIME FOR EFFICIENT LARGE-MAMMAL DENSITY ESTIMATION: GORILLAS AND DUNG HEIGHT

Hjalmar S. Kuehl,[1] Angelique Todd, Christophe Boesch, and Peter D. Walsh

Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103 Germany

Abstract. Large-mammal surveys often rely on indirect signs such as dung or nests. Sign density is usually translated into animal density using sign production and decay rates. In principle, such auxiliary variable estimates should be made in a spatially unbiased manner. However, traditional decay rate estimation methods entail following many signs from production to disappearance, which, in large study areas, requires extensive travel effort. Consequently, decay rate estimates have tended to be made instead at some convenient but unrepresentative location. In this study we evaluated how much bias might be induced by extrapolating decay rates from unrepresentative locations, how much effort would be required to implement current methods in a spatially unbiased manner, and what alternate approaches might be used to improve precision. To evaluate the extent of bias induced by unrepresentative sampling, we collected data on gorilla dung at several central African sites. Variation in gorilla dung decay rate was enormous, varying by up to an order of magnitude within and between survey zones. We then estimated what the effort–precision relationship would be for a previously suggested "retrospective" decay rate (RDR) method, if it were implemented in a spatially unbiased manner. We also evaluated precision for a marked sign count (MSC) approach that does not use a decay rate. Because they require repeat visits to remote locations, both RDR and MSC require enormous effort levels in order to gain precise density estimates. Finally, we examined an objective criterion for decay (i.e., dung height). This showed great potential for improving RDR efficiency because choosing a high threshold height for decay reduces decay time and, consequently, the number of visits that need to be made to remote areas. The ability to adjust decay time using an objective decay criterion also opens up the potential for a "prospective" decay rate (PDR) approach. Further research is necessary to evaluate whether the temporal bias inherent in such an approach is small enough to ignore, given the 10–20-fold increases in precision promised by a PDR approach.

Key words: decay rate estimation; decay rate heterogeneity; dung age; dung height; effort–precision relationship; gorilla; mammal density estimation; marked sign count; Normalized Difference Vegetation Index, NDVI; prospective decay rate; retrospective decay rate.

Introduction

Throughout the world large-mammal species are often surveyed using dung, nests, or other signs that they deposit. Examples include deer (Marques et al. 2001) and wild boar (Acevedo et al. 2006) in the northern hemisphere, kangaroos (Vernes 1999), wallabies (Johnson and Jarman 1987), and cassowaries (Westcott 1999) in Australia, and elephants (e.g., Barnes and Jensen 1987), antelopes, and many other elusive species (e.g., Plumptre 2000) in the subtropics and tropics.

A necessary aspect of using indirect signs in large-mammal surveys is translating sign density into animal density. This requires some assumptions about the number of signs deposited by each animal each day and the rate at which old signs become undetectable (the "decay rate"). The traditional approach has been to assume that both the sign production rate (p) and the rate at which signs decay are constant. Under this "steady-state" assumption, animal abundance can be estimated as

$$A = \frac{N}{p \times d}$$

where N is sign abundance and d the mean time from sign deposition to sign decay (Ghiglieri 1984, Tutin and Fernandez 1984).

A serious problem with the steady-state assumption is that it neglects the fact that as environmental conditions change through time so does sign decay rate (e.g., Barnes and Dunn 2002). When decay rate changes, the standing stock of signs does not equilibrate instantaneously. Rather, there is some transient period during which the number of signs decaying is not equal to the number being built. If this transient period is long relative to the time scale on which environmental conditions change, then the standing stock may rarely reach a steady state. This failure of the steady-state assumption creates serious biases for indirect count surveys of many species.

Manuscript received 5 June 2006; revised 4 April 2007; accepted 20 April 2007. Corresponding Editor: M. Friedl.
[1] E-mail: kuehl@eva.mpg.de

Two solutions to this problem have been proposed. The first is to estimate what Laing et al. (2003) refer to as a retrospective decay rate (RDR; see also Hiby and Lovell [1991]). In this approach freshly deposited signs are located during several regularly spaced sampling periods preceding a transect survey. All signs are then revisited at the beginning of the encounter rate survey to establish whether or not they have decayed. This method inherently integrates over decay rate heterogeneity in the period preceding the survey.

The second approach, the marked sign count (MSC), dispatches entirely with decay rate estimation (Hashimoto 1995, Plumptre and Reynolds 1996). It uses an initial visit to locate and mark all existing signs in a given transect detection zone and a second visit to evaluate how many new signs have been deposited during the inter-visit interval. Animal density is then estimated as the number of newly deposited signs divided by the product of the detection zone area, the length of inter-visit interval, and the daily sign deposition rate.

Although RDR and MSC reduce temporal bias by eliminating the steady-state assumption, they introduce a new problem (i.e., poor precision). Both approaches are imprecise because they require sampling of recently deposited signs, which account for only a small fraction of the standing stock. This means that the MSC requires much higher transect effort levels to gain a precise estimate of sign encounter rate than traditional standing stock methods. In the case of RDR, the high effort levels are required for decay rate estimation, not encounter rate estimation.

RDR also has low efficiency because sign decay rates vary spatially, not just temporally (Walsh and White 2005). Consequently, implementing RDR in an unbiased manner would require that sign decay samples be distributed representatively across a study area, not collected at some convenient location near a research camp or park headquarters. For small study areas with easy access this is achievable. However, for the vast roadless areas that are typical of regions such as central Africa, simply walking to remote sampling sites often chews up much more effort than the actual sampling. Furthermore, when sign decay times are long, each decay sampling visit requires a separate mission into a remote area. Thus, in large areas, implementing RDR in a spatially unbiased manner would require very high effort levels.

Here we use data we collected on surveys of western gorillas (*Gorilla gorilla gorilla*) to illustrate how serious the bias and precision problems associated with auxiliary variable estimation can be (see Plate 1). Many sources of information indicate a catastrophic decline of ape populations over the last decades (e.g., Ammann 2001, Butynski 2001, van Schaik et al. 2001, UNEP 2002, Huijbregts et al. 2003, Walsh et al. 2003, Kormos et al. 2004, Bermejo et al. 2006). Thus efficient survey methods are urgently needed for assessing the status of remaining populations in order to prioritize conservation actions or to evaluate their efficiency, success, or failure.

Unfortunately, the great apes are notoriously difficult to monitor (e.g., Plumptre and Reynolds 1996, 1997, Walsh and White 2005). Their cautious behavior, particularly in areas impacted by human activities, their low density, and the low visibility in their dense tropical forest habitat, make it difficult to monitor them via direct observations. Instead, signs of ape abundance are usually employed. The most frequently used signs are the sleeping nests apes construct each night (e.g., Tutin and Fernandez 1984, Hall et al. 1998), but for our study we used gorilla dung. Gorilla dung piles not only decay more quickly than gorilla nests, one also can use an objective criterion (dung height) in deciding whether or not a dung pile has "decayed." Using dung height eliminates another source of bias that has heretofore been ignored in ape surveys (i.e., intra- or inter-observer variation in defining whether or not a nest has decayed).

This paper is about spatiotemporal variability in gorilla dung decay, the effort–precision relationship of methods accounting for it when translating sign into individual abundance, and the advantage of using an objective decay criterion.

We start by using dung data we collected at several sites in Gabon, Republic of the Congo, and Central African Republic to quantify spatiotemporal heterogeneity in dung decay rate. In addition, we evaluate the effect of vegetation cover and rainfall on dung decay rate by using the Normalized Difference Vegetation Index (NDVI) as proxy variable. For freshly deposited dung piles we also model the effects of dung age and canopy cover on decay rate.

Second, we estimate the precision–effort relationship for RDR and MSC sampling. For RDR sampling, we assume that separate visits into the same remote area are required for sign sampling and transect survey, respectively.

Third, we examine how use of an objective criterion for decay (i.e., dung height) affects the precision of RDR. We do this by choosing a relatively high threshold that allows completion of all dung visits entailed in the RDR method in a single mission into a remote area.

Finally, we compare the precision of estimates obtained for RDR and MSC to those obtained through a prospective decay rate (PDR) approach. PDR uses the transect survey itself and one subsequent revisit to estimate decay rate. Because it uses all dung encountered on transects, not just fresh dung, it has the potential to be much more precise than the RDR or MSC method. However, PDR also requires a steady-state assumption, whose validity depends on how rapidly sign standing stock reaches equilibrium after decay conditions have changed. Here we use simulations to evaluate approximate durations of such transient periods for gorilla dung.

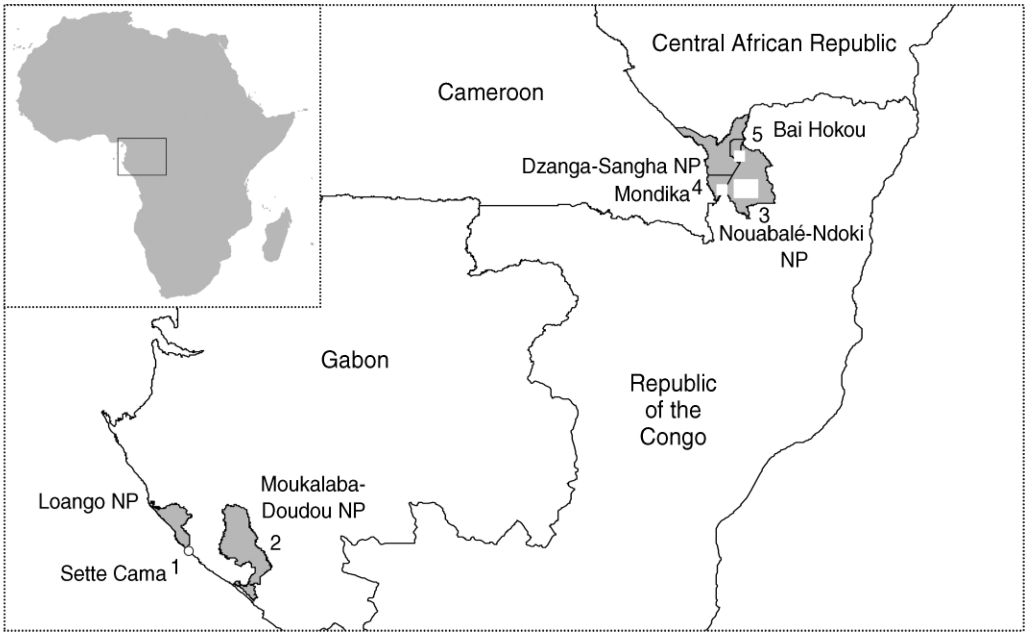

FIG. 1. Map of western equatorial Africa showing National Parks (NP) and sites where data for this study were collected. Sites: 1, Sette Cama; 2, Moukalaba-Doudou National Park (data were collected in the entire park); 3, Nouabalé-Ndoki National Park; 4, Mondika; and 5, Bai Hokou in Dzanga-Sangha National Park. For sites 3–5, sampling zones are indicated by white rectangles.

METHODS

Study sites

The data presented here were collected at five different sites in Gabon, Central African Republic, and Republic of the Congo (Fig. 1). The decay study on fresh gorilla dung piles was conducted south of Loango National Park next to Sette Cama village on the Atlantic coast of Gabon (January–April 2004). All other data were collected either in preparation for or during great ape surveys in Moukalaba-Doudou National Park, Gabon (April 2004–July 2005), and in the forest block of Sangha Tri-National-Park in Northern Republic of the Congo (Nouabalé-Ndoki National Park, October 2003–March 2004), and Central African Republic (Bai Hokou, July 2004 and January 2005, and Mondika study site, February 2005).

The Sette Cama study site is covered by a mosaic of coastal and lowland forest, savannah, and mangroves. The rugged Moukalaba-Doudou National Park is dominated by lowland and submontane tropical forest while the Sangha Tri-National-Park area is covered by dense tropical lowland forest with little topographic relief. The sites also differ in their rainfall patterns. All sites have two dry and two wet seasons each year, but the two Gabonese study sites are characterized by a boom-and-bust rainfall pattern with one intense rainy season and one long dry season (Thibault et al. 2001). Rainfall in the Sangha Tri-National-Park area is more evenly distributed throughout the year (Walsh and White 2005). However, fieldwork at the Sette Cama study site (2004) was characterized by an anomaly in the rainfall pattern. From January to May, a period of usually intense rain, the site received almost no precipitation.

Dung pile definition and decay criterion

One issue that needs to be addressed in using dung to estimate gorilla abundance is that feces from a single defecation event can be spread over several meters. Furthermore, feces from more than one defecation event are sometimes intermingled. Consequently, it is not possible to directly count defecation events during surveys. Rather, it is necessary to define some discrete sampling unit that can be identified consistently in both transect surveys and studies of dung production rates. Our sampling unit was the dung pile, which we operationally defined as one or more fecal boli not more than 10 cm apart. We chose this relatively short distance so as to avoid assigning dung deposited by different individuals to the same pile.

A second problem is the definition of when a dung pile has decayed. Traditionally dung was assigned to four or five decay categories (e.g., see Barnes and Jensen [1987] for elephants). Criteria for this classification were based on the appearance of the dung. However, this assignment is rather subjective and observer dependent. Here we use a new and objective criterion, dung height, to define the state of decay. We defined dung height as the vertical distance between the ground a dung pile was laying on and the maximum height of that pile. We constructed a caliper to measure dung height. The decay threshold (i.e., the height below which a dung pile was considered to be decayed) was then defined post hoc from the data set (see *Heterogeneity in dung decay rate: Definition of dung decay threshold*).

Collection of dung decay data

We located freshly deposited dung piles in the Sette Cama study area between January and March 2004 by searching for fresh sleeping nests and by tracking gorillas. We then measured the height of each dung pile. We revisited each dung pile up to 10 times at irregular intervals from one to seven days to re-measure height. Furthermore, we estimated canopy cover by taking an upward looking digital photo from a position 0.5 m above each dung pile.

Between October 2003 and July 2005 we collected decay data on dung of all ages during great ape surveys at the various sites (Moukalaba-Doudou National Park, Nouabalé-Ndoki National Park, Bai Hokou, and Mondika) using only two visits. Dung piles were first detected during normal transect sampling (Buckland et al. 2001) and height was measured. A second visit to each dung pile was then used to re-measure dung height.

Choosing an appropriate inter-visit interval is critical because the precision of the dung decay estimate is low if too many or too few dung piles decay between visits. To determine a suitable inter-visit interval we conducted a pilot study in September and October 2003 in Nouabalé-Ndoki National Park. During this pilot study we searched for dung piles in a 2×2 km study zone within the park. We then revisited the dung piles up to 10 times, 1–14 days later and re-measured height each time. On basis of this pilot study we decided to do revisits 1–10 days after the detection of dung piles during transect sampling.

Heterogeneity in dung decay rate

Definition of dung decay threshold.—As a first step in the analysis of the collected data we defined a dung decay threshold height of 2.5 cm for the data from the Sette Cama site. This height was low enough to minimize exclusion of dung piles with low initial height (only two piles out of 79), while high enough to ensure that an intermediate number of dung piles decay during the study period. For the decay data from all other sites we defined a decay threshold of 3.5 cm to balance this trade-off. These data were collected with slightly different protocols, and data quality was not as consistent as for the Sette Cama data set. We therefore had to exclude 30% of the dung piles (226 out of 761) with height at first visit below 3.5 cm.

Covariate information.—Rainfall influences dung decay in two ways. It mechanically breaks down dung and it influences microbial decomposition, which is dependent on ambient humidity. Vegetation structure influences both of these processes, however in contrary ways. Mechanical decomposition by rain decreases with increasing vegetation density and canopy cover. Humidity affecting microbial decomposition is better conserved with increasing vegetation and canopy cover (Masunga et al. 2006).

A consequence of this interaction between canopy structure and rainfall is heterogeneity in dung decay rate, which translates into uncertainty in estimates of dung decay rate. One way to reduce this uncertainty is to statistically explain the variation of replicate samples by incorporating environmental covariates. The advantage of this approach is that the uncertainty of decay rate estimates is reduced if powerful predictors of dung decay can be identified (e.g., Barnes and Dunn 2002).

We tested three sources of covariate information: ground measurements of canopy cover, satellite derived Normalized Difference Vegetation Index (NDVI), and dung pile age. We used digital photographs to estimate canopy cover for each dung pile. We imported the photos into Adobe Photoshop, Version 8.0, and converted them to black and white images. The histogram function in Photoshop was then used to determine the percentage of black pixels (canopy cover, hereby referred to as CC) in each image.

Our second covariate was NDVI, which is correlated with vegetation structure and composition as well as the amount of rainfall (e.g., Goward et al. 1991, Eklundh 1998, Richard and Poccard 1998). We used NDVI scores derived from Spot-satellite imagery, which are downloadable for free from the internet.[2] Each image had a spatial resolution of 1 km and a temporal resolution of 10–11 days. We extracted the NDVI values for each dung pile location with the GIS/Remote Sensing software IDRISI 32 (Eastman 2001).

The Sette Cama study was conducted in the dry season when there was little mechanical breakdown of dung by rain. We were, therefore, only interested in the vegetation structure effect on decay and used the original NDVI scores directly. For all other studies, we used NDVI as an index of rainfall. To filter out local differences in vegetation structure and composition we normalized the original NDVI values (dividing each value by the yearly NDVI mean for that same location). Our hope was that variation in these normalized NDVI values would be correlated with rainfall variation.

The age of a dung pile was defined as the time interval between date of dung deposition and date of revisit. Different studies (e.g., Laing et al. 2003) have shown that probability of sign decay changes with age. Hence, it is crucial to also incorporate this variable in decay rate models.

Covariate modeling of decay rate of fresh dung.—We used the fresh dung pile data from Sette Cama to develop a model of how environmental covariates and dung age affect the decay process of gorilla dung for two reasons. First, we wanted to know whether decay probability would be age dependent or not. Second, we were interested in whether or not environmental

[2] ⟨www.vgt.vito.be⟩

covariates could be used to predict dung decay probability.

We used two generalized linear modeling approaches to estimate how the three environmental covariates influenced dung decay probability. In the first approach we treated time as continuous and assumed that the probability that a dung pile would still be above a defined threshold height t days after it was deposited followed a logistic function:

$$f(t) = \frac{\varepsilon^{b_0+b_1x_1+b_2x_2+b_3x_3+b_4t}}{1+\varepsilon^{b_0+b_1x_1+b_2x_2+b_3x_3+b_4t}} \quad (1)$$

where t is the time interval between visits, $x_1 - x_3$ are the mean values of the three covariates (age, CC, and NDVI) over time interval t, and the b's are coefficients to be estimated. We also considered the possibility of age dependence in decay rate. To represent the case in which dung decay is dependent on age (a) we inserted into Eq. 1 a second-degree polynomial:

$$b_5a + b_6a^2.$$

In the second approach we assumed that dung decay was a first-order Markov process with daily time steps (i). In this case, the probability that a dung pile survived from one day to the next was predicted by Eq. 1 with the time-dependent term removed. The survival probability over any time interval t was then just the product of the discrete daily survival probabilities $p(i)$:

$$p(0,t) = \prod_{i=0}^{i=t} p(i). \quad (2)$$

We estimated the parameter values for both the continuous and discrete models using the dung pile data from Sette Cama. For each dung pile that decayed during our study, we used Eqs. 1 and 2 to predict the likelihood that it survived to the last visit before decay and the first visit after decay. Subtracting these two quantities,

$$1 - p(i,j) = f(i) - f(j) \quad (3)$$

gave the likelihood that the dung decay event fell in the observed inter-visit interval. For dung piles that did not decay during the study, the likelihood was just the survival probability at the last visit.

For both logistic and Markov models, we found the maximum likelihood values for the b's using the user-specified loss-function of the nonlinear regression routine in SPSS, Version 13.0 (SPSS 2004). We also fitted a null model in which dung decayed at a constant rate that was not affected by the covariates. To compare models we used Akaike's information criterion (AIC), with the 95% model confidence set defined to include those models whose cumulative Akaike weight was equal to 0.95 (Burnham and Anderson 2002).

We also estimated mean decay times (mean life span) μ_x. We used two approaches: (1) the continuous RDR approach presented by Laing et al. (2003), and (2) a discrete time approach in which we calculated the products of the probability of dung decay on each day and the time after deposition and then summed values over time,

$$\mu_x = \sum_{t=0}^{t\to\infty} t \times [p(t) - p(t-1)] \quad (4)$$

with $p(t)$ as the decay probability on day t. We then derived confidence intervals by bootstrapping with 1000 resamples.

Covariate modeling of decay rate of dung of all ages.—For evaluating spatial heterogeneity in dung decay rate we used the same model-fitting procedure as described above for the Sette Cama study (see *Methods: Covariate modeling of decay rate of fresh dung*). We tested global models in which all sites shared a common decay rate parameter against local models, which allowed different dung decay rate parameters for each site. Because information on canopy cover was not available for all dung piles at all sites, we used only NDVI as a covariate. In addition, mean dung height differed between sites, perhaps as a consequence of between-site differences in gorilla diet. Dung height should presumably affect dung decay probability. Therefore, we included mean dung height as an additional covariate to predict the daily decay probability.

Prospective decay rate (PDR) using two visits.—The daily rate of change in the standing stock of dung piles (ΔY) represents a competition between the rate at which dung piles are deposited fN (f is the daily defecation rate, N is the number of gorillas) and the rate at which they disappear dY (d is the daily dung pile decay rate, Y is the standing stock of dung piles). For a short time period with no change in animal density, we can further assume that the system of dung deposition and dung decay is in balance and has reached steady state (McClanahan 1986). We can write

$$0 = fN - dY. \quad (5)$$

The daily disappearance rate d can be calculated as the mean decay probability:

$$d = \sum_{n_i=1}^{n_i=j} z_i \times [1 - p(x_i)] \quad (6)$$

where z_i is the proportion of dung surviving with probability $p(x_i)$. Gorilla abundance can then be calculated from Eq. 6 as follows:

$$N = \frac{Y_0 \times d}{f} \quad (7)$$

where Y_0 is the standing stock at first visit, and f is the daily dung pile deposition rate (A. F. Todd, H. S. Kuehl, C. Cipolletta, and P. D. Walsh, *unpublished manuscript*).

Relative efficiency of methods

To evaluate the relative efficiency of the three methods we calculated coefficients of variation (CVs) for each method across a range of survey effort levels.

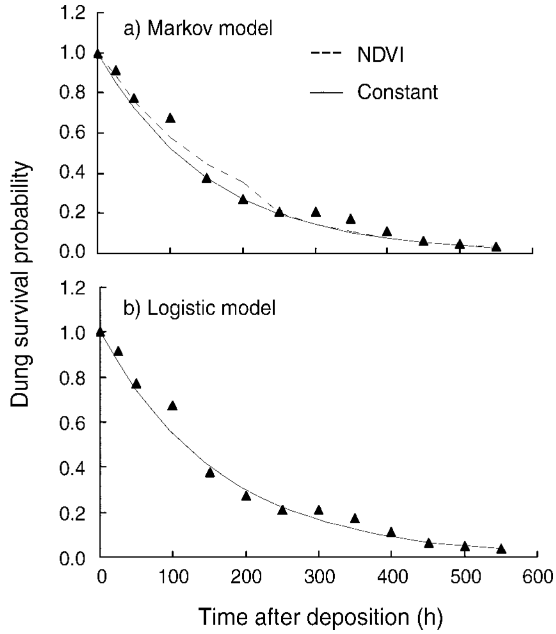

FIG. 2. Observed and predicted cumulative probability of gorilla dung survival over time. Data are from the Sette Cama study area. Triangles show the observed proportion of dung surviving to a given time. The first data bin is 25 hours, and subsequent bins are 50 hours. In panel (a), the solid curve represents a Markov model with constant decay probability; the dashed line shows the NDVI (Normalized Difference Vegetation Index) Markov model predictions. Panel (b) depicts a logistic time-only model.

These precision estimates considered both dung decay rate (for RDR and PDR) and dung encounter rate variances, which we combined using the Delta Method (Seber 1982). We did not include the variance in defecation rate, which is the subject of another paper (A. F. Todd, H. S. Kuehl, C. Cipolletta, and P. D. Walsh, *unpublished manuscript*). Given that all three methods require defecation rate estimates, this omission should not bias the results towards one method.

Decay rate variances for PDR and RDR were estimated by bootstrapping data from the Sette Cama data set. To estimate encounter rates and their variances, we used the standing stock data from our largest survey data set (Nouabalé-Ndoki National Park). For the PDR method we used all dung piles in the standing stock when estimating encounter rate. For the RDR method we used Eq. 6 to estimate the proportion of dung that was fresh each day, and then multiplied this proportion by the total encounter rate to find the encounter rate for fresh dung. For the MSC method we conservatively reasoned that a two-day inter-visit interval would be short enough to avoid having dung piles deposited after the first visit decay but before the second. We therefore assumed that the MSC encounter rate would be equal to twice the daily dung deposition rate estimated for RDR.

To predict how the coefficients of variation for each of the three methods should vary with survey effort we assumed linear variance inflation (Buckland et al. 2001):

$$\hat{b} = \frac{\widehat{\mathrm{var}}}{n}.$$

For each method, the constant b was estimated from the appropriate empirical data set then projected over a range of effort levels.

This initial estimate of RDR precision was based on the assumption that each sampling of a dung pile would require a separate mission into a remote area. To evaluate how much RDR precision might improve by using dung height as an objective criterion of decay, we assumed that two samples could be made on the same mission. Given that sampling within remote sites occupied only about one-third of the days in the Nouabalé-Ndoki National Park study, this assumption implies that using an objective criterion should double the amount of sampling possible in a single mission while increasing effort by only 33%: total effort = within site effort + residual effort $= 2 \times 1/3 + 2/3 = 4/3$, as opposed to the doubling of effort that would be required for two separate missions. Thus, we recalculated the RDR variance inflation factor (b) assuming that the sampling effort necessary to achieve the observed estimate variance was 67% as high, $(4/3)/2 = 0.67$. We then reprojected the precision effort relation using this inflation factor.

Dung decay time reduction and transient period

Threshold height vs. sample size.—We examined the relationship between dung threshold height and the number of dung piles going over this threshold within a predefined time period. Increasing the threshold height increases the number of dung piles crossing the threshold, which decreases deviation from steady state. However, it also increases the number of dung piles whose initial height is below the threshold height. Hence, the crucial issue is to balance the bias reduction accrued by reducing decay time with the precision loss resulting from smaller sample size.

To search for an optimal balance, we used the data set collected at the Sette Cama study site. We defined a time period of 22 days, which in central African biomonitoring programs is approximately the duration of a field mission to a remote area. For a range of threshold heights, we calculated both the proportion of dung piles with initial height above the threshold and the proportion of dung piles not decaying within this time period.

Transient periods.—We defined the transient period as the time required for gorilla dung standing stock to reach 95% of its steady-state value (approximately equal rates of dung deposition and decay) after a change in decay conditions. We used simulations to evaluate transient periods for both changes from high to low decay probabilities (wet to dry seasons) and low to high decay probabilities (dry to wet seasons). As low decay probability we used the decay probability we estimated from the Sette Cama data set, which was collected

TABLE 1. Results of covariate modeling of the decay rate of fresh gorilla dung from the Sette Cama study area.

Model	Intercept	Covariates				No. parameters	AIC	w_i
		Time	Age	NDVI	CC			
Markov	5.649		0.071	−0.035		3	256.1	0.59
Markov	4.979		0.069	−0.035	0.009	4	257.8	0.25
Markov	5.599			−0.031		2	259.7	0.10
Markov	4.466			−0.031	0.015	3	260.8	0.06
Null	1.788					1	282.3	0.00
Logistic	−15.331	−0.006				2	283.6	0.00

Notes: Listed are the four models in the 95% Akaike weight confidence set, as well as a null model and a logistic time-only model. Covariates are time, dung pile age, Normalized Difference Vegetation Index (NDVI), and canopy cover (CC). The number of estimated parameters, Akaike's Information Criterion (AIC), and Akaike weight (w_i) are also reported.

during a period with almost no rain. As high decay probabilities we used probabilities 25%, 50%, and 100% higher than the one for Sette Cama. All decay models used for the simulation included an age term.

We simulated the standing stock of gorilla dung by introducing six new dung piles every day. We started each run by imposing one decay probability for 50 days (i.e., a time interval great enough for the standing stock to reach steady state). At day 51 we replaced the decay probability with a higher or lower probability. We then evaluated how long it took the standing stock to reach at least 95% of the new long-term mean standing stock value under the new decay conditions.

RESULTS

Heterogeneity in dung decay rate

Covariate modeling of decay rate of fresh dung.—Fresh dung piles from the Sette Cama study area decayed at a high rate (Fig. 2). Fifty percent of the piles in our sample ($N = 77$) decayed within 120 hours (five days). Ninety-five percent of all dung piles had fallen below the decay threshold height of 2.5 cm after 21 days.

Adding age dependence to the models improved the fit to the data substantially (Table 1). Also the inclusion of NDVI and canopy cover provided improvement in fit (21–27 AIC units) over both a null model assuming that there was no relationship between inter-visit interval and decay probability and a model assuming logistic time dependence but no covariate effects (Table 1). The 95% Akaike weight confidence set of models includes four Markov models, with the first two of them containing the variable age. Logistic models were not included in the confidence set.

The parameter estimate for the variable age was positive, which implies that dung piles decay slower with increasing age. Increasing NDVI values increased decay probability, while increasing canopy coverage slowed it down.

Mean decay time estimates based on either a summation over discrete time intervals (in hours) or numerical integration over continuous time gave similar results (Table 2). Estimated mean decay time differed among models, with 155 hours for the Markov model and 167 hours for the logistic time-only model. This is a difference of about 7%. The coefficients of variation (CV) for mean decay time were 11% and 17%, respectively.

Covariate modeling of decay rate of dung of all ages.—In all cases, local models fit the dung decay data better than global models (Table 3). Models with separate parameter estimates for each of the five sites had AIC values 21–42 units lower than the best global models. Furthermore, covariate models including NDVI effects fit the data better than models assuming no NDVI effects. The 95% confidence set contained three NDVI models, two Markov and one logistic. They accounted for 65%, 19%, and 11% of Akaike weight, respectively.

The best-fitting global NDVI models were Markov models containing mean dung height as site-specific covariate information. Their AIC values were >50 units lower than the global null model. However, the addition of NDVI to the mean height model did not produce a substantive improvement in fit.

The implications of the superiority of local models are evident in a comparison of site-specific decay curves (Fig. 3). Gorilla dung survival probability estimated from a set of local time-only models varied tremendously between the different survey sites. The two extreme sites differ by almost an order of magnitude in daily dung survival probability. In contrast, the survival probabilities from the Moukalaba-Doudou survey and the Nouabalé-Ndoki pilot study were almost identical. They are represented in Fig. 3 as only one curve.

Temporal variation in dung decay probability is also evident in the two curves representing successive surveys in Bai Hokou, Central African Republic, during the rainy (July) and dry season (January). Daily dung decay

TABLE 2. Mean decay time estimates for gorilla dung.

Model	μ_x (hours)	CV(μ_x)	95% CI (hours)
Markov	155	0.11	125–195
Logistic, linear	167	0.17	112–212

Notes: Estimates (identical for continuous time and discrete approach) are based on time-only models with integration over 10^4 hours. Abbreviations: μ_x, mean decay time in hours; CV(μ_x), coefficient of variation for mean decay time; and 95% CI, confidence intervals based on bootstrapping with 1000 resamples.

TABLE 3. Results of covariate modeling of decay rate of dung of all ages at different central African survey sites.

Model	Intercept	Covariates in the model				No. parameters	AIC	w_i
		1	2	3	4			
Markov, local	constant		lag 0	lag 1		18	472.0	0.65
Markov, local			lag 0	lag 1		12	474.5	0.19
Logistic, local	constant	time	lag 0	lag 1		24	475.6	0.11
Null, local	constant					6	481.5	0.00
Logistic, local	constant	time				6	493.5	0.00
Markov, global	constant		lag 0		height	3	514.6	0.00
Markov, global	constant				height	2	515.3	0.00
Markov, global	constant					1	571.8	0.00

Note: Key to abbreviations: lag 0 is NDVI during first visit; lag 1 is NDVI 10 days before first visit; height is mean dung height for survey site; AIC is Akaike's Information Criterion; w_i is Akaike weight.

probability in the wet season is almost five times higher than in the dry season (Fig. 3).

Relative efficiency of methods

The three methods varied greatly in terms of their precision–effort trade-off (Fig. 4). In order to achieve the same target coefficient of variation the RDR and MSC methods require effort levels that are several times higher than for the PDR method.

However, the efficiency of RDR can be increased drastically by decreasing dung decay time, which allows sign decay sampling and encounter rate surveys to be conducted during the same mission to a remote sampling location (RDR II, Fig. 4).

Dung decay time reduction and transient period

Threshold height vs. sample size.—As expected, the reduction of gorilla dung decay time was a trade-off between minimizing the exclusion of dung piles with low initial height from the data set and maximizing the proportion of dung piles going over the threshold within a predefined time period (Fig. 5). Setting a threshold height of 3.4 cm insured that all dung piles in the Sette Cama data set were below the threshold height after 22 days. However, 30% of dung piles had initial heights below the threshold and, therefore, would be excluded from a decay rate estimate. Dropping the threshold height to 2.5 cm results in a better compromise, with 95% of dung below the threshold in 22 days but only 3.5% excluded because of low initial height.

Transient periods.—In our simulation experiment gorilla dung standing stock relaxed rapidly to steady state after decay probabilities were changed (Fig. 6). As one might expect, transient periods were longer when decay probabilities change from high to low (Fig. 6b) than from low to high (Fig. 6a). Transient periods ranged from six to 19 days after changes in decay probability from low (Sette Cama decay probability) to high (1.25×, 1.5×, or 2× Sette Cama decay probability). A decrease in decay probability generated transient periods of 19–28 days.

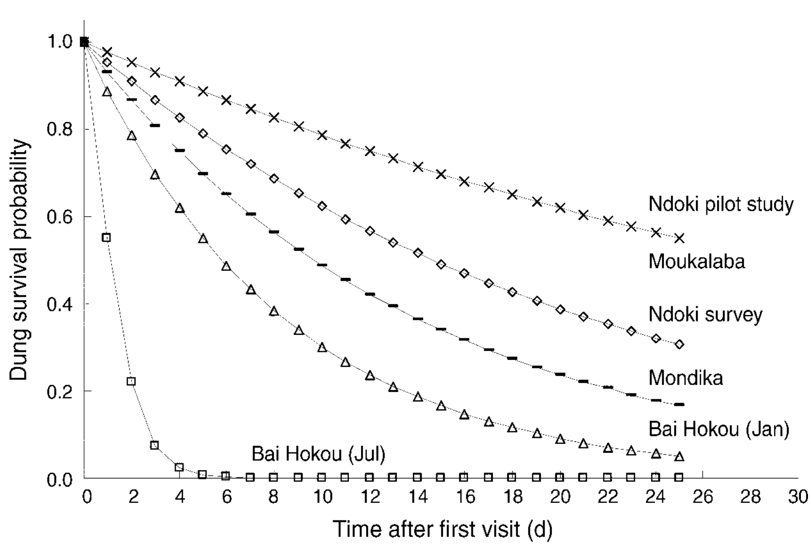

FIG. 3. Cumulative probability of dung survival at different central African study sites. Decay rates of dung from the Nouabalé-Ndoki pilot study and the Moukalaba-Doudou survey were almost identical and are represented as a single curve. Bai Hokou was sampled in two seasons: dry (January) and rainy (July). The *x*-axis label refers to time after the first visit by observers.

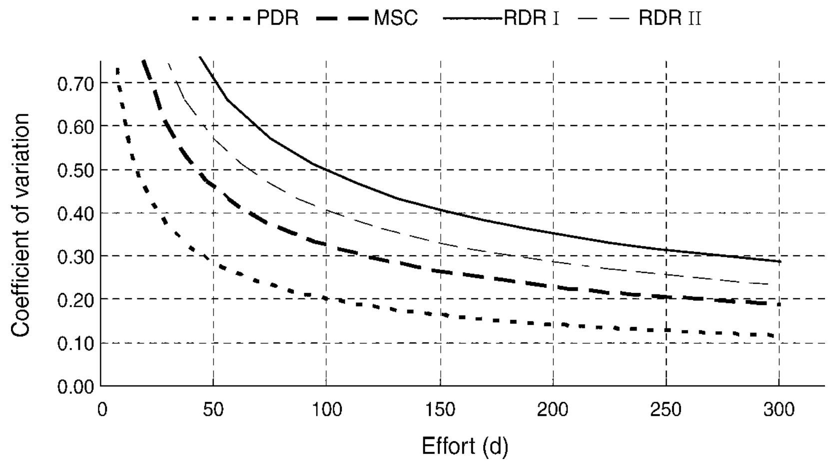

FIG. 4. Effort–precision relationship of retrospective decay rate (RDR), marked sign count (MSC), and prospective decay rate (PDR) methods. For PDR, MSC, and RDR I, effort (number of days) is based on the mean number of transects (equivalent to 1-km segments) sampled during our study per day (1.3 transects per day). RDR I represents a sampling scheme with repeated trips to each remote location. RDR II represents a scenario with reduced dung decay time. Here we combined several sampling cycles in one period of travel, which increases the mean daily number of transects sampled to two.

Discussion

Three important results emerge from our study. First, we found very substantial spatial heterogeneity in gorilla dung decay rates. Such spatial heterogeneity is not peculiar to gorilla dung but flows from the fundamental tendency for the environmental conditions that determine sign decay rates to vary at virtually all spatial scales (e.g., Walsh and White 2005). Consequently, the pervasive tendency to extrapolate decay rate estimates derived from studies in convenient locations to large survey zones is likely inducing large biases in abundance estimates for many large-mammal species.

Our second major result is that one of the most promising new options for ape survey, the retrospective decay rate (RDR) method, has low precision when applied in a spatially unbiased manner. Because the method requires several visits into each remote area to find fresh signs, travel effort is prohibitively high, given the large size of many Central African survey zones. This is a serious problem for surveys based on any slowly decaying sign, such as ape nests or elephant dung for example. These problems with low encounter rates and multiple visits also apply to the marked sign count (MSC) method, however to a lesser extent.

Our third major result is that a viable solution to the problem of multiple visits may lie in switching to dung as an index of gorilla abundance, then shortening decay time by using dung height as an objective criterion of decay. Reducing decay times to one to three weeks means that both decay rate estimation and encounter rate sampling can be accomplished during the same mission into each remote area. Because travel into remote areas represents a high proportion of overall survey effort in large protected areas, using dung with a threshold height has the potential to radically increase the precision of the RDR method.

One cost of shortening sign decay time is that dung decay rate estimation should not be done too close to encounter rate sampling because the tendency to scare animals during dung decay rate sampling could have a substantial impact on subsequent encounter rate sampling in the vicinity. Using separate transects for dung encounter sampling and dung decay rate estimation increases survey effort for the RDR method, but not nearly as much as the distinct missions into remote areas that would be required for signs that decay. Parenthetically, the tendency to scare animals during the "sign marking" visit to each transect gives us some doubt about whether or not the MSC method could be applied to gorilla dung in an unbiased manner. We see no comparable way of alleviating this problem.

The use of an objective dung decay criterion has one further advantage. Making decay times arbitrarily short opens the possibility of prospective decay rate (PDR)

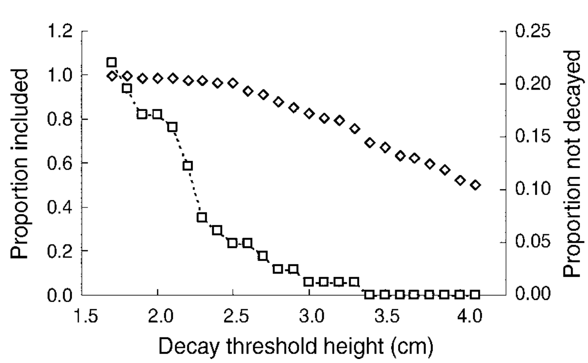

FIG. 5. Trade-off between inclusion of dung piles with low initial height (diamonds, left axis) and inclusion of dung piles going over a threshold height (squares, right axis) during a predefined transient period of 22 days. Data are from the Sette Cama study site.

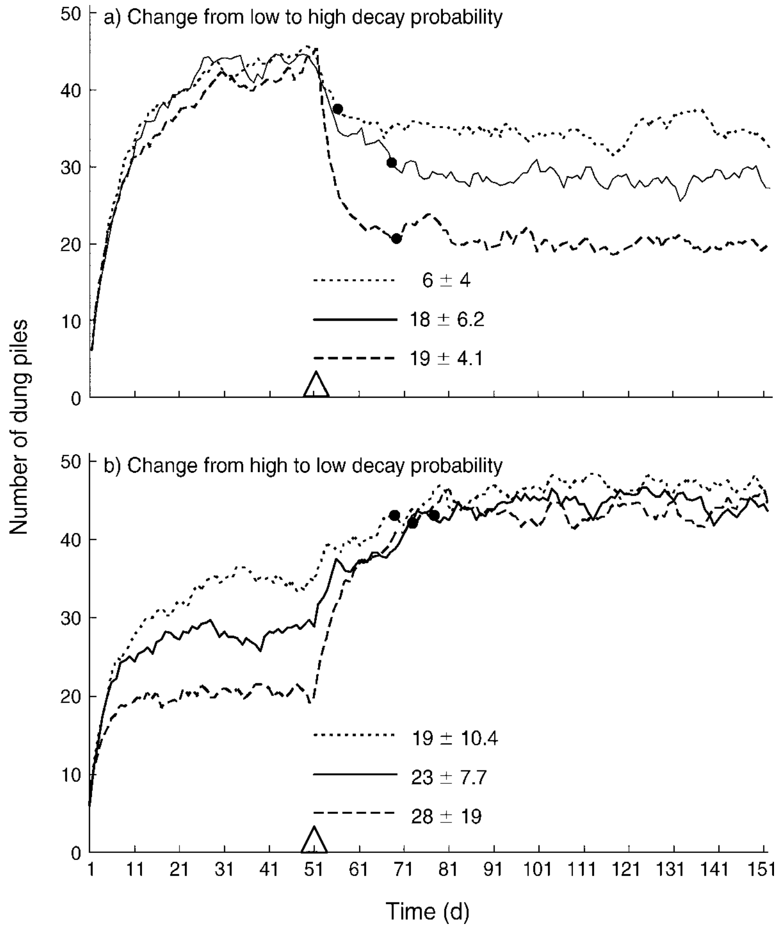

FIG. 6. Determination of length of transient periods through simulation. Graphs show simulated gorilla dung standing stock, to which six new dung piles were introduced each day. (a) During the first 50 days, decay probability was estimated from the Sette Cama data set (dry season). From day 51 (triangle) onward, decay probability was replaced by probabilities that were 25% (dotted line), 50% (solid line), or 100% (dashed line) higher than the one from Sette Cama. In panel (b), decay probabilities were changed from high to low. Black dots indicate the point at which standing stock reaches the 5% boundary around the long-term mean value. Parallel lines represent the length of transient periods (mean ± SD, in days) for different curves starting at day 51.

estimation. The preliminary results we presented here suggest considerable promise for the combination of dung and PDR. We were able to choose a threshold decay height that produced a rapid decay time while excluding only a small proportion of dung. This, in combination with the fact that PDR uses all dung encountered not just fresh dung, gives PDR a high precision. One problem of PDR sampling is that age, as an important predictor of decay probability, is unknown for dung encountered on transects. However, our analyses suggest that most of the age dependence of dung decay probability apply later in the dung decay process. Thus, setting a high threshold height may help to reduce the effect of age dependence.

What remains to be seen is exactly how much bias is introduced assuming that the decay conditions following the detection of a dung pile are equivalent to those before. We intended to study this issue but an abnormally dry period during our study prevented us from collecting enough data to adequately estimate the effects of rainfall heterogeneity on dung decay rates. We therefore recommend the following studies to more comprehensively and definitively evaluate whether the bias involved in using the PDR approach can be minimized enough to make its superior precision worth pursuing.

A several month time series of gorilla dung decay rate data or any other rapidly decaying sign needs to be collected. This time series should cover periods of varying decay conditions and not just a dry period as in our study. With this time series two objectives can then be addressed. First, a covariate model can be fitted to the data as we did for our study. Preferably this covariate model should include rainfall, which is known to be one of the major determinants of dung decay at other times than dry periods (e.g., Barnes et al. 1997,

PLATE 1. Western lowland gorilla silverback (*Gorilla gorilla gorilla*) at a forest clearing in Bai Hokou, Central African Republic. Photo credit: Chloe Cipolletta, World Wildlife Fund-Central African Republic.

Barnes and Dunn 2002). The covariate model can then be used to simulate sign standing stock and PDR sampling. Such simulation will permit the evaluation of the amount of bias inherent in a PDR approach. Second, it will also allow a better assessment of the effect of dung age on decay rate. Such information would be helpful in determining whether the absence of information on sign age would induce serious bias in estimates made using PDR sampling.

We also see potential for inverting the prospective approach described here to produce what is essentially a retrospective estimate of dung decay rate. This would still use the first visit to a transect to estimate encounter rate but the decay events recorded by the second visit would now be used to estimate a model relating decay probability to values of environmental covariates (NDVI, rain, etc.). This covariate model would then be used to make retrospective dung decay estimates for each transect, given the environmental conditions prevailing before the first visit.

We also suggest testing objective decay criteria for other signs and species. Different signs may require another criterion than height (e.g., diameter, volume, or potentially in the case of nests, spectral properties). Finally, we suggest a comparative study of the PDR method and the existing nest count methods, standing crop and marked nest count, which we could unfortunately not include in our analysis due to the lack of data.

ACKNOWLEDGMENTS

This project was financed by the Max Planck Society, National Science Foundation (NSF-DEB 0213001), Deutscher Akademischer Austauschdienst, Rufford Foundation, and World Wildlife Fund-Gabon. We thank the government of Gabon for allowing us to work in the Gamba-Complex of protected areas, including Loango and Moukalaba-Doudou National Parks, the government of the Republic of Congo for permission to collect data in Nouabalé-Ndoki National Park, and the government of the Central African Republic for allowing us to conduct our research in Dzanga-Sangha National Park. In the Central African Republic we were supported by the World Wildlife Fund and would like to thank Chloe Cipolletta, the BaAka trackers, and student volunteers. We further thank Diane Doran for letting us collect data at the Mondika field site. Our work in Nouabalé-Ndoki National Park was only possible through the generous logistical and administrative support that Wildlife Conservation Society-Congo infrastructure and personnel provided. Data collection there was only possible with great support by Aime Bassouama, Destin Mangola, Rene Ngotto, Yano Sylvain, Pierre Gombo, and research coordinator Emma Stokes. For our work in Gabon we thank especially Brice Leandre Meye, Park Warden of Moukalaba-Doudou National Park, for his full support, and Augustin Mihindou Mbina, Park Warden of southern-Loango National Park and president of the Technical Management Committee during the time of field work, for his huge efforts in coordinating conservation work in the larger Gamba Complex. We also had great personnel and administrative support from World Wildlife Fund-Gamba through Bas Huijbregts, Marc Dethier, Stephane Le Duc Yeno, Hugues Mouanambatsi, and Christian Nzeingui and his survey team. We are also thankful for very helpful comments on the manuscript from Carsten Dormann and two anonymous reviewers.

Literature Cited

Acevedo, P., J. Vicente, U. Höfle, J. Cassinello, F. Ruiz-Fons, and C. Gortazar. 2006. Estimation of European wild boar relative abundance and aggregation: a novel method in epidemiological risk assessment. Epidemiology and Infection 135:519–527.

Ammann, K. 2001. Bushmeat hunting and the great apes. Pages 71–85 *in* B. Beck, T. S. Stoinski, M. Hutchins, T. L. Maple, B. Norton, A. Rowan, E. F. Stevens, and A. Arluke, editors. Great apes and humans: the ethics of coexistence. Smithsonian Institution Press, Washington, D.C., USA.

Barnes, R. F. W., B. Asamoah-Boateng, J. Naada Majam, and J. Agyei-Ohemeng. 1997. Rainfall and the population dynamics of elephant dung-piles in the forest of southern Ghana. African Journal of Ecology 35:39–52.

Barnes, R. F. W., and A. Dunn. 2002. Estimating forest elephant density in Sapo National Park (Liberia) with a rainfall model. African Journal of Ecology 40:159–163.

Barnes, R. F. W., and K. L. Jensen. 1987. How to count elephants in forests. IUCN African Elephant and Rhino Specialist Group Technical Bulletin 1:1–6.

Bermejo, M., J. D. Rodríguez-Tejeiro, G. Illera, A. Barroso, C. Vilà, and P. D. Walsh. 2006. Ebola outbreaks kills 5000 gorillas. Science 314:1564.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, Oxford, UK.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Butynski, T. M. 2001. Africa's great apes. Pages 3–56 *in* B. Beck, T. S. Stoinski, M. Hutchins, T. L. Maple, B. Norton, A. Rowan, E. F. Stevens, and A. Arluke, editors. Great apes and humans: the ethics of coexistence. Smithsonian Institution Press, Washington, D.C., USA.

Eastman, J. R. 2001. IDRISI for Windows. Version 32; release 2.0. Clark University, Worcester, Massachusetts, USA.

Eklundh, L. 1998. Estimating relations between AVHRR NDVI and rainfall in East Africa at 10-day and monthly time scales. International Journal of Remote Sensing 19:563–568.

Ghiglieri, M. P. 1984. The chimpanzees of Kibale forest: a field study of ecology and social structure. Columbia University Press, New York, New York, USA.

Goward, S. N., B. Markham, D. G. Dye, W. Dulaney, and J. Yang. 1991. Normalized difference vegetation index measurements from the Advanced Very High Resolution Radiometer. Remote Sensing of Environment 35:257–277.

Hall, J., et al. 1998. A survey of Grauer's gorilla (*Gorilla gorilla graueri*) and chimpanzee (*Pan troglodytes*) in Kahuzi-Biega National Park and adjacent areas in Democratic Republic of Congo. International Journal of Primatology 19:207–235.

Hashimoto, C. 1995. Population census of the chimpanzees in the Kalinzu forest, Uganda: comparison between methods with nest counts. Primates 36:477–488.

Hiby, L., and P. Lovell. 1991. DUNGSERV—a program for estimating elephant density from dung density without assuming "steady state." Pages 73–79 *in* U. Ramakrishnan, J. A. Santosh, and R. Sukumar, editors. Censusing elephants in forests: proceedings of an international workshop. Asian Elephant Conservation Centre, Bangalore, India.

Huijbregts, B., P. De Wachter, L. S. Ndong Obiang, and M. E. Akou. 2003. Ebola and the decline of gorilla (*Gorilla gorilla*) and chimpanzee (*Pan troglodytes*) populations in Minkebe Forest, north-eastern Gabon. Oryx 37:437–443.

Johnson, C. N., and P. J. Jarman. 1987. Macropod studies at Wallaby Creek. 6. A validation of the use of dung-pellet counts for measuring absolute densities of populations of macropodids. Australian Wildlife Research 14:139–145.

Kormos, R., C. Boesch, M. I. Bakarr, and T. Butynski. 2004. Chimpanzés d'Afrique de L'Ouest. Etat de conservation de l'espèce et plan d'action. Group de spécialistes des primates de la CSE de L'UICN, Gland, Suisse et Cambridge, UK.

Laing, S. E., S. T. Buckland, R. W. Burn, D. Lambie, and A. Amphlett. 2003. Dung and nest surveys: estimating decay rates. Journal of Applied Ecology 40:1102–1111.

Marques, F. F. C., S. T. Buckland, D. Goffin, C. E. Dixon, D. L. Borchers, B. A. Mayle, and A. J. Peace. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. Journal of Applied Ecology 38:349–363.

Masunga, S. G., O. Andresen, J. E. Taylor, and S. Dhillion. 2006. Elephant dung decomposition and coprophilus fungi in two habitats of semi-arid Botswana. Mycological Research 110:1214–1226.

McClanahan, T. R. 1986. Quick population survey method using faecal droppings and a steady state assumption. African Journal of Ecology 24:37–39.

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

Plumptre, A. J., and V. Reynolds. 1997. Nesting behavior of chimpanzees: implications for censuses. International Journal of Primatology 18:475–485.

Richard, Y., and I. Poccard. 1998. A statistical study of NDVI sensitivity to seasonal and interannual rainfall variations in Southern Africa. International Journal of Remote Sensing 19:2907–2920.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Macmillan, New York, New York, USA.

SPSS. 2004. SPSS for Windows. Version 13.0. SPSS, Chicago, Illinois, USA.

Thibault, M., P. D. Walsh, D. Idiata, C. Mbinda, Y. Mihindou, and L. J. T. White. 2001. Inventaires des grands mammifères dans le complexe d'aires protégées de Gamba en 1998 et 1999. Rapport préliminaire. World Wildlife Fund, Central Africa Regional Program Office and Wildlife Conservation Society, Libreville, Gabon.

Tutin, C. E. G., and 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.

UNEP. 2002. Great apes: the road ahead. C. Elleman and A. Newton, editors. A GLOBIO perspective on the impacts of infrastructural development on the great apes. United Nations Environment Programme.

van Schaik, C. P., K. A. Monk, and J. M. Yarrow Robertson. 2001. Dramatic decline in orang-utan numbers in the Leuser Ecosystem, Northern Sumatra. Oryx 35:14–25.

Vernes, K. 1999. Pellet counts to estimate density of a rainforest kangaroo. Wildlife Society Bulletin 27:991–996.

Walsh, P. D., et al. 2003. Catastrophic ape decline in western equatorial Africa. Nature 422:611–614.

Walsh, P. D., and L. J. T. White. 2005. Evaluating the steady state assumption: simulations of gorilla nest decay. Ecological Applications 15:1342–1350.

Westcott, D. A. 1999. Counting cassowaries: What does cassowary sign reveal about their abundance? Wildlife Research 26:61–67.