Using Dung to Estimate Gorilla Density: Modeling Dung Production Rate

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Abstract There is an urgent need for information on western gorilla population sizes and distribution to improve present and plan future conservation actions. Researchers traditionally have estimated gorilla densities on the basis of nest counts despite demonstrated variation in nest production and decay rates. The variation may lead to large biases in estimates of gorilla abundance. We investigated the use of an alternate index of gorilla abundance, via defecation data collected from habituated gorillas at Bai Hokou, Central African Republic. Our sample of 274/370 defecation events/dung piles produced a production rate of *ca.* 5 dung piles/d: comparable to previous estimates based on much smaller sample sizes. Heuristic models that failed to account for imperfect dung pile detection produced a lower defecation rate estimate than that of a maximum likelihood model that explicitly modeled detection probability. Generalized linear modeling (GLM) showed that dung pile production rate was strongly linked to rainfall, suggesting that failure to correct for seasonal variation in dung pile production rates could lead to substantial biases in gorilla abundance estimates. In our study, failing to distinguish between the number of defecation events and the number of dung piles produced would lead to a *ca.* 31% overestimate of true gorilla numbers. The use of dung as an index of gorilla abundance shows potential, but more fieldwork and modeling on seasonal variation in dung production rates is required.

Keywords dung · gorilla density · model · survey

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Introduction

Throughout Central Africa, western gorilla populations are seriously threatened by deforestation, the bushmeat trade, and diseases such as Ebola hemorrhagic fever. Ape populations have declined drastically in the last 2 decades (Walsh *et al.* 2003); a recent outbreak of Ebola in Congo caused a massive die-off (ca. 5000 gorillas: Bermejo *et al.* 2006). However, despite increased conservation efforts, only limited information is available on how many western gorillas remain or their distribution. The information is urgently needed and fundamental to assess and to improve the efficiency and effectiveness of future conservation actions.

The lack of information results largely from the inherent difficulties of monitoring individuals in dense forests. Directly observing gorillas is difficult, and researchers traditionally have estimated gorilla densities on the basis of nest counts, combined with data on nest production and nest decay rates (Bermejo 1999; Blake *et al.* 1995; Blom *et al.* 2001; Brugiere and Sakom 2001; Carroll 1988; Fay 1989; Fay *et al.* 1989; Furuichi *et al.* 1997; Poulsen and Clark 2004; Remis 2000a; Tutin and Fernandez 1984; Williamson and Usongo 1996). The estimates are frequently extrapolated and are the basis of our present knowledge on the large-scale distribution of western gorillas.

However, the calculations involve assumptions about nest building behavior that may be invalid. For example, nest group size might not be a good estimator of ape group size; researchers might not detect all nests, and single gorillas can produce >1 night nest (Mehlman and Doran 2002; Remis 1993; Tutin *et al.* 1995). Also, many density estimates relied on a single study of nest decay rate (Tutin and Fernandez 1984), even though decay rate can show high spatiotemporal variation. Extrapolating biased nest production and decay rates over huge survey areas leads to large inaccuracies in estimates of gorilla abundance (Walsh and White 1999). Thus improved or new methods are critical for more accurate measures of gorilla distribution and abundance.

One alternative is to use dung as an index of gorilla abundance. Dung has long been an effective means to survey elusive forest species, including small animals, macropods, ungulates, and forest elephants (Barnes 2000; Barnes *et al.* 1997; Fuller 1991; Merz 1986; Nchanji and Plumptre 2001; Neff 1968; Plumptre and Harris 1995; Tchamba 1992; Walsh and White 1999). Gorilla dung piles are more numerous and decay faster than nests, which is more in keeping with the steady-state assumption on which researchers have based most gorilla densities (McClanahan 1986; Kuehl *et al.* 2007).

Previous estimates of gorilla defecation rates are few, and come mostly from captive studies of gut passage rates wherein diets are low in fiber and environmental conditions poorly resemble those in the wild (Caton 1999; Lambert 2002; Milton 1999; Remis 2000b). Schaller (1963) estimated that wild mountain gorillas defecated ≥ 5.51 times/d; they deposited half the dung boli at or near nest sites (based on 2-d follows of 2 lone silverbacks and investigation of 4 group nest sites). The only estimate for western gorillas, whose diet differs greatly from that of mountain gorillas, was a minimum of 3–5 defecations at Lopé (Tutin *et al.* 1991). Rogers *et al.* (1998) also noted a high proportion of western gorilla dung deposited at nest sites.

Besides small sample sizes, there was a very narrow window of environmental conditions on which to base the defecation rate estimates. One should relate the amount and timing of fecal output to feeding behavior and gut passage time (Warner 1981). Defecation rate may also vary with season (rainfall), diet (proportion of fruit vs. nonreproductive plant parts), age, and health (White and Edwards 2000).

Our aim was to provide improved daily defecation rate estimates for western gorillas. We modeled individual dung production rate to estimate the number of defecation events and dung piles produced on each observation day by habituated gorillas at Bai Hokou, Central African Republic (CAR). We also used data on fruit availability, rainfall, and a remotely sensed measure of vegetation greenness [normalized differenced vegetation Index (NDVI)] to investigate seasonal variation in daily dung production rates. Finally, we assessed the relative usefulness of counting defecation events versus counting dung piles, and evaluated the threshold distance defining when 2 dung boli are treated as different piles during surveys. Our ultimate goal is to provide less biased methods for translating transect data into gorilla density estimates.

Methods

Study Site and Subjects

Bai Hokou (2°51'34"N, 16°28'03"E) is within the Dzanga-Ndoki National Park (1240 km²) in southwestern CAR. The Dzanga-Sangha Protected Areas (DSPAs), a collaboration between the CAR Government, the World Wide Fund for Nature (WWF) and GFA Terra Systems consult (for the German Technical Cooperation, GTZ), manages the park, together with the Dzanga-Sangha Special Dense Forest Reserve (3159 km²). Bai Hokou is the base of the Primate Habituation Programme, where the habituation of gorillas for tourism has been ongoing since 1997 (Blom *et al.* 2004). We collected dung deposition data during follows of the well-habituated Munye group, comprising a silverback and his subadult son (*ca.* 6.5 yr). The Munye group regularly accepted observers at close range, allowing prolonged visibility (>80% of 15-min scan samples: Cipolletta *et al.* 2007). We could accurately assign the origin of all dung piles based on dung lobe size alone (Schaller 1963).

Dung Deposition: Detection for Defecation Rate

We located the gorillas by tracking their footprints and food remains from nest to nest with the help of skilled BaAka trackers. The gorillas remained in or nearby their nests between 1800 and 0600 h. We split tracking into morning (0700–1200 h) and afternoon (1200–1700 h) teams. We collected defecation data in 1 or both of the periods on ≥ 5 d/mo over 10 mo from October 2003 to July 2004.

Dung data fall into 2 categories: dung piles from directly observed defecation events and ones as traces post-event. We assumed that gorillas had just deposited all dung piles found as traces, other than those at night nests, and reduced any error in the assumption by allocation *post hoc* of dung piles to the hour in which we found

them. We assumed that dung piles at nests were deposited from 0600 to 0700 h, before the gorillas left their nests. We easily distinguished dung from the previous night or evening from morning dung by: dryness, hardness, and state of decay, including that from dung beetles. As we could not accurately determine the timing of the evening dung piles, we pooled all such dung into a single class, for which we estimated production rate separately.

For both gorillas we collected data on: 1) the time of each event or if a trace, the time of location; 2) the individual's position (ground or tree height) during direct observations; 3) habitat type: monodominant forest of *Gilbertiodendron dewevrei*, mixed species forest, riverine forest, forest of Marantaceae spp., light gaps, forest clearings, logging roads, and transitional phases between them; 4) dung pile height; 5) distance between different dung piles from the same event (≥ 0.1 m); 6) minutes of direct observation per morning or afternoon sampling period.

Analysis

Modeling daily dung production rate For each individual, we estimated the number of dung piles produced during the 10 daylight observation hours heuristically by dividing the number of directly observed dung piles (N) produced during a given morning by its duration (F , in hours), then multiplying by the proportion of the morning in which we directly observed the focal gorilla (O). We then multiplied the hourly production rate by the number of observation hours (10), to estimate a daily, diurnal production rate (N_d)

$$N_d = 10 (O (N/F)). \quad (1)$$

We followed an analogous procedure for all afternoon sessions, then averaged N_d across all mornings and afternoons.

Using observed dung piles only would potentially underestimate dung production rate if we missed some dung piles deposited while gorillas were out of view. Feeding records and data on mean gut retention times of captive individuals (Caton 1999; Milton 1999; Remis 2000b; Remis and Dierenfeld 2004) indicate that peak production rate should occur mostly at night or early morning, precisely when the gorillas were out of visual contact (feeding peaks 0700–1000 h and 1300–1700 h; Fig. 1). We thus performed the same procedure using trace data instead. To accommodate trace data and allow diurnal variation in production rate we used a linear modeling approach. We started with a simple baseline model assuming that during daylight hours, gorillas produced dung piles at a constant hourly rate (A). For the model, the predicted number of dung counted during a given morning or afternoon of length T is

$$N = ATO + AT(1 - O)D, \quad (2)$$

wherein D is the probability that we detected a dung pile gorillas deposited when not in direct visual contact. We used a GLM (nonlinear regression module of SPSS version 13.0 assuming Gaussian error) to estimate values for hourly production rate, A , and detection probability, D , simultaneously from direct observation and trace data. We then multiplied by 12 to arrive at a daily dung pile production rate estimate.

Fig. 1 Percentage frequency activity per hour per individual: solid lines, silverback; dashed lines, subadult; squares, % time feeding; triangles % time resting.

We used 3 approaches to represent the predicted morning peak in production rate. First, we simply fitted separate morning and afternoon dung pile production rates (A_a and A_m). Second, we assumed that for the first hour of the morning, production rate increased by an increment (B) above the background production rate (A). This changed our hourly defecation estimator of the morning to

$$N = (A + B) T_6 O + (A + B) T_6 (1 - O) D + AT_{7+} O + AT_{7+} (1 - O) D \quad (3)$$

wherein T_{7+} is the number of follow hours after 0700 h. Third, instead of adding a discrete increment in production rate, we assumed that for the first 3 h of the day production rate declined according to a Gaussian function:

$$f(t) = A + B e^{-\frac{(t-6)^2}{2s^2}}.$$

This gives

$$N = (AT_{9+} O + AT_{9+} (1 - O) D + \sum_{t=6..8} (f(t) O + f(t) (1 - O) D)), \quad (4)$$

Note that in all the approaches the values of O , the proportion of time that gorillas were in direct visual contact, were specific to each hour or group of hours. For all 3 approaches, we considered models with all combinations of detection probability and dung production rate, including separate detection probabilities for morning and afternoon periods.

To obtain 95% confidence intervals (CI) for each dung pile production rate estimate, we bootstrapped the data ($N=113$ morning or afternoon sampling periods). To compare different models, we used Akaike's information criterion (AIC, Burnham and Anderson 2002). To arrive at our final estimates of dung pile production rate we averaged estimates from different models via the Akaike weight

method. Estimates in Table III incorporate evening dung pile and defecation events, which we estimated as simple means for each individual (as in Eq. 1).

Environmental covariate modeling To explore seasonal variation in dung pile production rate, we used several environmental factors as covariates in a GLM. To reduce stochastic variation we pooled data into 10-d sampling periods ($N=23$ 10-d sampling periods) and predicted the total number of dung produced during each period. The covariates were: the average number of fruit species found in daily dung samples; average daily rainfall (using sampled days only); average daily rainfall from 3 d previous to the day of dung sampling (reduced feeding activity during heavy rain may result in reduced fecal output 2–3 d later); total rainfall for the 10-d period; and NDVI data (with a spatial resolution of 1 km and a temporal resolution of 10 d, <http://free.vgt.vito.be/>). NDVI is a measure of canopy greenness correlated with rainfall, vegetation structure, and leafing phenology. Because there is often a time lag in the effect of weather on phenological patterns such as fruiting (Shinoda 1995), we also considered NDVI values from 3 mo before dung sampling.

In the GLM, we estimated daily dung output as the sum of the number of direct observations and the normalized number of trace observations, i.e., observed number divided by the detection probability from the model average, corrected for observation effort on that day and averaged over each 10-d sampling period. We implemented the covariate model via a best-subsets GLM, with a log link function and Gaussian error, in Statistica version 7.1. For each gorilla, we chose best models and evaluated the relative importance of each covariate evaluated on the basis of AIC and Akaike weight (Burnham and Anderson 2002). We examined effect sizes of highly weighted covariates by evaluating the relative dung production rates predicted by the lowest and highest observed values for a given covariate.

Dung piles vs. defecation events The fecal material produced in single defecation events does not always fall in 1 pile, particularly during defecations from trees and while moving. A method to enumerate defecation events from dung pile counts is necessary to ensure that the counts on transect surveys correspond to ones counted in dung production rate studies. The simplest approach is to define a dung pile as a cluster of fecal material that is separated from other fecal material by more than some threshold distance. Short threshold distances minimize bias arising from treating dung deposited by multiple gorillas as a single pile, but reduce estimate precision because the coefficient of variation in the number of dung piles produced per day increases as threshold distance decreases. This can confound estimates of seasonal variation in defecation rate and reduce the precision of dung production rate estimates based on covariate modeling.

Accordingly, we repeated our daily dung pile production rate and covariate modeling based on defecation rates. To convert daily defecation rates into estimates of dung pile production rates we multiplied by the mean number of dung piles produced per defecation event, which we estimated using both directly observed events and traces. To compare the precision of the covariate modeling, we considered all models within the 95% Akaike weight confidence set. We derived standard errors (SE) for each parameter by bootstrapping the data and used the δ

method (Seber 1982) to estimate a global SE for each model. We then calculated Akaike weight averaged SEs across models.

Results

Dung Deposition

We recorded 274 defecation events that produced 370 dung piles on 96 d (dry season $N=33$ d, wet season $N=63$ d), including 75 morning and 38 afternoon sampling periods. We detected more defecation events and dung piles as traces than we observed directly (Table I). Dung piles from the 2 individuals were easily distinguishable [average fresh dung height silverback (SB), 6.48 cm, SE 0.16 and subadult (SA), 4.20 cm, SE 0.13; Fig. 2), and similar to the dung diameters per Schaller (1963: SB >7.3 cm, juvenile 4–5.4 cm). The proportion of average hourly follow time gorillas were in direct visual contact was greater in the afternoon and for the silverback (SB morning=0.41, SB afternoon=0.49, SA morning=0.32, SA afternoon=0.39). There was a large proportion of dung piles at nests (SB 53%, SA 42%). Most of them were in Marantaceae forest (SB 69%, SA 65%) and non-nest dung piles were mostly in mixed forest (SB 82%, SA 86%).

Heuristic Estimates of Defecation Rate

Pooling direct observations and traces gave the silverback a higher rate for both defecation and dung pile production (Table II). Defecation rates varied diurnally for both individuals (Fig. 3). Peak morning and midday rates coincided with their departure from the night nests and the end of a rest period between 1000 and 1300 h (Fig. 1). Defecations were at the silverback's nest on 96% of days, but only on 35.5% of days for the subadult. Defecations from the previous evening were not so prevalent (SB 27.6% of days, SA 14.5% of days); hence evening defecation rates were low (SB 0.29 defecation events, CV 0.16, and 0.41 dung piles, CV 0.23; SA 0.16 defecations events, CV 0.24, and 0.20 dung piles, CV 0.30). When we add them to the previous estimates from daily data, total daily defecation rates are 4.51 and 3.39 for the silverback and subadult respectively, and 6.28 and 4.12 for dung pile production rates.

Table I Number of defecation events versus dung piles from direct observation and trace data

	Defecation events			Dung piles		
	Direct	Trace	Total	Direct	Trace	Total
Silverback	38	132	170	41	194	235
Subadult	34	70	104	26	109	135

Fig. 2 Frequency of individual dung pile heights in 0.5-cm categories: black bars, silverback; gray bars, subadult.

Maximum Likelihood Modeling

For the silverback, 3 dung pile models accounted for 93% of the Akaike weight (Table IIIa). The best fitting model (41% of Akaike weight) assumed a single dung pile production rate for the entire day but different detection probabilities for morning and evening. The model-averaged estimates showed little difference in dung production rate between morning and evening, but estimated a higher detection probability in the morning (Table IV). All models produced similar daily dung pile production rates, with a model-averaged estimate of 5.03 dung/d (including evening dung, 95% CI 3.99–10.64 dung/d).

For the subadult (Table IIIb), we chose a slightly different set of models. In contrast to the heuristic approach, the model-averaged daily dung pile production rate (5.57 dung piles/d, 95% CI 2.08–12.03 dung/d) was similar to that for the silverback. Because the heuristic method failed to correct for the subadult's much lower trace dung detection probability, it underestimated subadult dung pile production rate.

Results for the analyses based on defecation events, rather than dung piles, produced comparable results (Table IIIc and d). Defecation rate estimates for

Table II Daily defecation and dung pile production rates from direct observation and trace data

	Defecation events			Dung piles		
	Direct	Trace	Pooled	Direct	Trace	Pooled
Silverback	1.44 (30)	2.77 (12)	4.22 (12)	1.83 (39)	4.04 (11)	5.87 (11)
Subadult	1.79 (29)	1.45 (17)	3.23 (18)	2.11 (18)	2.56 (16)	3.92 (13)

Numbers in parentheses indicate sample sizes.

Fig. 3 Mean defecation rate per hour per individual (smoothed): solid lines, silverback; dashed lines, subadult.

Table III Estimates for the different daily and afternoon defecation (A and A_a) and detection probability (D and D_a) model parameters

A	A_a	D	D_a	Dung/d	AIC	Cumulative Akaike wt
a. Silverback dung pile models						
0.39		0.96	0.58	5.14 (4.27–10.24)	474.14	0.41
0.37			0.92	4.89 (3.94–7.73)	474.36	0.73
0.42	0.33		0.87	4.88 (3.62–14.67)	474.85	0.93
0.38	0.46	1.00	0.41	5.47 (3.66–14.92)	475.90	1.00
				5.03 (3.99–10.64)		
b. Subadult dung pile models						
0.35	0.55	0.31		5.58 (1.92–12.66)	404.36	0.73
0.28	0.61	0.52	0.19	5.56 (2.56–10.98)	405.64	0.93
0.43		0.20	0.50	5.34 (2.43–8.43)	407.00	0.98
0.45		0.25		5.65 (2.14–8.66)	407.98	1.00
				5.57 (2.08–12.03)		
c. Silverback defecation event models						
0.34		0.63		4.31 (2.40–9.48)	331.73	0.52
0.34		0.65	0.47	4.41 (2.88–8.82)	332.35	0.80
0.35	0.32	0.61		4.30 (1.82–8.71)	333.16	0.92
0.30	0.40	0.81	0.32	4.49 (2.29–9.93)	333.61	1.00
				4.36 (2.46–9.26)		
d. Subadult defecation event models						
0.21	0.39	0.48		3.77 (0.65–8.12)	329.89	0.82
0.18	0.41	0.63	0.42	3.74 (1.32–8.09)	331.72	0.95
0.29		0.26	0.85	3.58 (1.74–7.64)	332.83	1.00
0.32		0.34		3.99 (1.95–9.24)	340.49	1.00
				3.75 (0.78–8.08)		

Dung/d includes evening defecation rates; confidence intervals are shown in parentheses; model averaged value at the bottom.

Table IV Model-averaged parameter estimates for the different daily and afternoon defecation (A and A_a) and detection probabilities (D and D_a)

	Defecation event models				Dung pile models			
Parameter	A	A_a	D	D_a	A	A_a	D	D_a
Silverback	0.34	0.34	0.65	0.56	0.39	0.38	0.93	0.73
Subadult	0.21	0.39	0.49	0.49	0.34	0.55	0.35	0.29

different models were again similar within and between gorillas. The detection probability difference between silverback and subadult narrowed, because the higher probability of finding ≥ 1 dung pile from an event had a greater impact for the subadult.

Modeling Daily Defecation Rate with Environmental Covariates

For both individuals, covariate models fit the data better than the assumption of constant dung pile production or defecation rate (best dung pile model SB AIC=88.29, null AIC=98.73, SA AIC=28.45, null AIC=30.99; best defecation event model SB AIC=88.41, null AIC=91.19, SA AIC=15.01, null AIC=22.04). Overall, defecation event models produced more precise estimates than dung pile models (averaged dung pile models SB CV=0.091, SA CV=0.177; averaged defecation event models SB CV=0.065, SA CV=0.084).

In all 4 analyses (SB\SA $\times$ piles\events), the best model accounted for a large proportion of the Akaike weight. Two covariates were particularly well represented in the 95% model confidence sets: average daily rainfall and total rain for the 10-d period. Rainfall on the day of sampling correlates positively with both dung pile production and defecation rate, whereas rain for the entire 10-d period correlates negatively. Effect sizes for the covariates tended to be large. For the silverback's best defecation event model, predicted defecation rate was 2.37 times higher for the highest observed average daily rainfall than for the lowest. Likewise, predicted defecation rate increased by a factor of 2.41 over the observed range of 10-d rainfalls.

Number of Piles Per Defecation Event

The distance between consecutive dung piles from the same event differed between individuals (SB mean=0.62 m, SE 0.010; SA mean=0.36 m, SE 0.010). The majority of defecation events occurred on the ground (SB 97%, SA 80%), most of which comprised 1 pile ≤ 0.1 m (SB 50%, SA 65%). The subadult defecated from trees more often than the silverback did (SB 3%, SA 20%), with a higher production of multiple-pile events from trees (SB 25%, SA 65%). This may be a function of sample size (SB=8, SA=26) or height (the silverback's most frequent height when defecating from trees was 0–5 m whereas the subadult's was 5–10 m). Using observations and traces together gave a higher number of piles per event (observations and traces SB 1.38, SA 1.31; observations only SB 1.11, SA 1.26).

Discussion

We confirm the potential of dung as an index of gorilla abundance. Despite diurnal variation, dung production rate estimates were fairly consistent between the subadult and silverback and similar to previous estimates based on lower sampling effort (Schaller 1963; Tutin *et al.* 1991). We have also shown that covariate modeling of easily collectable environmental data can explain substantial variation in defecation and dung pile production rates, thus promising to increase estimate precision and reduce bias. However, several other issues remain before one can establish dung as an index for gorilla density estimation.

Seasonal Variation

Perhaps the greatest issue is seasonal variation in defecation and dung pile production rates. Our generalized linear modeling results imply strong seasonal influences on dung production rates. For 2 of 4 best models the improvement in model fit produced by the covariates was moderately large, with AIC decreases of 10.4 and 7.1. More importantly, the effect sizes for major covariates were large, with predicted defecation and production rates more than doubling over the observed range of covariate values. Rainfall was particularly important and appeared to influence dung production rates in 2 opposing ways. First, dung production rates correlate positively with rainfall on the day of sampling. It is not clear whether this was due to an actual increase in the rate of defecation on rainy days or to an increased probability of dung detection because the gorillas moved less on rainy days. Our approach of first estimating dung detection probability, then using it to model variation in production rates did not allow us to tease apart the 2 explanations. Doing so would require customized analysis software that embedded the detection probability model within a generalized linear modeling and model selection framework. Because we wanted to make our analysis accessible and easily repeatable with available statistical software, we did not pursue such an analysis.

In contrast, dung production rates declined with increasing 10-d rainfall, which may reflect a dry season increase in rates of fiber consumption. Fiber increases gut passage rates in both chimpanzees and humans (Milton 1999) and leads to increased fecal output (Warner 1981). However, the defecation rate of forest elephants, whose diet closely resembles that of gorillas, is higher in the wet season (Ruggiero 1992). Further study is needed to investigate whether seasonal differences in defecation rates are due to changes in dietary quality or the sheer amount of food ingested.

In any case, the effects of rainfall on dung production rates imply that assuming a constant defecation rate (Barnes 2001; Barnes *et al.* 1997; Fuller 1991; Merz 1986; Neff 1968; Plumptre and Harris 1995; Tchamba 1992) produces biased density estimates. For example, we used transect surveys at Bai Hokou to estimate a wet season gorilla dung density of 32/km² (Todd, *unpub. data*) and a daily dung decay probability of 0.28/d (Kuehl *et al.* 2007). Dividing the product of the 2 estimates by our mean dung pile production rate estimate of 5.3/d gives a gorilla density estimate of 1.7/km². However, if we use the GLM results to predict a wet season-specific production rate of 9.2 dung piles/d, then the gorilla density estimate shifts to 0.98/km².

Thus, using a mean dung production rate estimate instead of a seasonally adjusted estimate biases the gorilla density estimate upward by 73.5%.

Detection Probability

We highlight the difficulties inherent in collecting field data on rare behavioral events, such as defecation, even from well-habituated individuals. Theoretically, closely following focal subjects should make measuring defecation rates easy. However, researchers cannot observe many defecation events directly and may or may not detect them, leading to underestimates of dung production rates.

The problem was particularly acute for the subadult, whose smaller dung lobe size and greater tendency to defecate from trees, and from greater heights, increased the chances that we overlooked dung piles. Maximum likelihood modeling suggests that failing to account for imperfect detection probability could underestimate subadult dung pile production rate by *ca.* 30%, which would translate into a 30% overestimation of subadult gorilla density. The models estimated much higher dung pile detection probabilities for the silverback and, consequently, less potential for overestimation of silverback density. As adult female dung lobe size and arboreality are intermediate between subadults and silverbacks, the potential for overestimating density should also be intermediate. In summary, more investigations to cover age- and sex-specific estimates of dung detection probability are required to convert dung density to gorilla density reasonably accurately.

Defecation Events Versus Dung Piles

Distinguishing between the number of defecation events and the number of detectable dung piles is important. In our study, failing to recognize that defecation events produced an average of 1.34 dung piles would lead to a *ca.* 31% overestimate of true gorilla numbers. Therefore, we caution against using typically overestimated defecation rates from captive individuals when converting dung encounter rates into densities. We recommend that researchers using dung count studies on other species, e.g., antelopes and elephants, should also address the issue (Chapman 2004; Dhungel 1985; *cf.* Laing *et al.* 2003; Webbon *et al.* 2004).

The use of an appropriate threshold distance may reduce the error. Most dung piles from the same event were ≤ 10 cm of each other, suggesting it as a reasonable threshold distance for defining piles. Modeling defecation events, rather than dung piles, also seems to provide more precise estimates of covariate effects on dung defecation rate.

Diurnal Variation

A final issue is diurnal variability in dung production rate. Defecation patterns of hominids and most primates have a 24-h cycle: most feces are eliminated in the early morning, with a marked reduction in output during the afternoon and none during the night (this study; Caton 1999; Heaton *et al.* 1992; Julliot 1996; Lambert 2002). Studies that do not apply sampling designs or analyses that account for diurnal variation risk biasing their estimates.

In conclusion, we provide the first nonanecdotal estimates of the rate at which western gorilla defecate in their natural environment. We show that one can use habituated gorillas to estimate defecation rates rigorously and that season has a strong effect on defecation rate, which one can control for via environmental covariate modeling. Still, confidence intervals on production rates were large and estimates were based on only 2 individuals. Therefore, we encourage more studies that include both more individuals and all sex/age classes.

Also meriting further study is the effect of habitat variation on defecation rate. Given that defecation rate varies with diet, it seems likely that spatial variation in distribution of food species is linked to variation in defecation rate. Unfortunately, there are very few western gorilla groups that are well-enough habituated for accurate defecation rate estimation. Therefore, it will be impossible to estimate defecation rates that are particular to the habitat distribution at each and every survey site. Instead, the best option would be to use data on observed habitat variation within and among habituated groups to estimate a habitat model similar to the rainfall model we described. The accuracy of such an endeavor will depend on the extent to which researchers can group habitats into a small number of generic classes that accurately capture the mechanistic relationship between habitat type and gorilla defecation rate. Whether this will be ultimately possible is an empirical question that can be answered only by applying well-defined estimation and model validation methods to more extensive empirical data.

Finally, the issue of spatiotemporal variation in production rates is not particular to dung, but equally applicable to other signs of subject abundance, though researchers have largely ignored it in the case of ape sleeping nests. It is vital to resolve the issue in a timely fashion to estimate gorilla population sizes accurately and to detect how fast populations are declining in order to plan effective conservation interventions.

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