

# Forest elephant dung decay in Ndoki Forest, northern Congo

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## Abstract

The decay of elephant dung piles has been shown to be a complex process. Rainfall has been attributed as the main factor influencing dung pile survival in various central African forests. This study monitored elephant dung piles from deposition to disappearance to show that dung survival in Ndoki Forest in northern Congo is mainly influenced by the intensity of irradiance and minimum temperature in the days after deposition. This could lead to substantial differences of dung decay in pristine forest compared with logged forest with a disturbed canopy, and care should be taken when applying rainfall models to calculate dung decay rates. On-site surveying of elephant dung piles covering all habitat types should therefore be undertaken before any elephant dung survey is conducted.

**Additional key words:** density estimates, *Loxodonta africana cyclotis*, monitoring, rainfall, rainforest

## Résumé

Il a été démontré que la dégradation des crottes d'éléphants est un processus complexe. On a montré que dans les forêts d'Afrique Centrale, la quantité de pluie tombée est le facteur principal qui influence la durée de visibilité des crottes d'éléphants. Dans cette étude nous avons suivi la dégradation des crottes du jour de leur déposition jusqu'à leur disparition afin de montrer que dans la forêt de Ndoki située au Nord Congo, la dégradation est principalement influencée par l'intensité de solaire et la température minimale dans les jours qui suivaient leur déposition. Ce qui pourrait conduire à des différences appréciables vis-à-vis la dégradation des crottes dans les forêts intactes et les forêts perturbées. Par conséquent, il faut faire attention en appliquant les modèles de la pluie (« rainfall models »). Avant chaque inventaire sur la densité des éléphants, il est recommandé d'étudier la dégradation des crottes dans le site d'étude.

**Mots clés supplémentaires :** estimations de densité, *Loxodonta africana cyclotis*, monitoring, pluie, forêt dense

## Introduction

Despite intensive conservation efforts, the future of African forest elephants (*Loxodonta africana cyclotis*) is unsure. This is due to numerous threats such as ivory poaching and loss of habitat but also we lack reliable estimates of population size throughout their range (Blake et al. 2007).

The remote Ndoki Forest of the Sangha Trinational Conservation Landscape is one of the last intact

forest blocks in central Africa. It harbours one of the largest remaining populations of forest elephants (Blake et al. 2007). Several hundreds up to thousands of elephants have been identified in forest clearings in the region (Vanleeuwe et al. 1998; Turkalo and Fay 2001; Inkamba Nkulu 2005; Mbeli Bai Study, long-term data). However, logging around the protected areas is increasing at a dramatic rate and pressure on the elephant population is continuous because of illegal poaching for ivory (Blake et al. 2007; Carpe

2007). Population estimates are therefore essential to monitor the status of elephants in the region.

Forest elephants are difficult to observe in the dense rainforests of western and central Africa. Therefore indirect survey methods such as dung counts along line transects are used to calculate elephant dung density (Merz 1986; Barnes and Jensen 1987; Plumptre 2000; Eggert et al. 2003 for a genetic survey). To convert dung-pile density to elephant density it is important to calculate dung decay rate (assuming defecation rates are known) (Barnes and Jensen 1987). Decay of elephant dung is a complex process and the use of dung decay rates from other sites or even different seasons can lead to false estimates of elephant densities. Seasonal variation in dung decay is caused by different environmental variables, particularly rainfall (Barnes et al. 1997; Nchanji and Plumptre 2001), and rainfall models have been proposed that can be used to estimate elephant numbers (Barnes and Dunn 2002). Also, the amount of fruit in the diet, the type of habitat, the microclimate where the dung is deposited, and the abundance and diversity of decomposers (particularly fungi and dung beetles) are important factors that regulate dung decomposition (White 1995; Barnes et al. 1997; Nchanji and Plumptre 2001; Mubalama and Sikubwabo 2002; Barnes et al. 2006; Masunga et al. 2006). In addition to this within-site variation, dung decay estimates vary substantially between sites (Nchanji and Plumptre 2001). Using decay rates from other sites can therefore be problematic and on-the-site studies are recommended for each dung survey (Hedges and Lawson 2006).

By knowing the factors affecting dung survival one can better plan the timing and duration of an elephant survey to avoid sampling in seasons with different environmental conditions affecting dung survival. In this study, we monitored the exact duration of elephant dung piles to describe factors affecting dung survival around Mbeli Bai in the south-west of Nouabalé-Ndoki National Park. We investigated how some of the factors mentioned above affect dung survival. Additionally

we included an alternative factor, solar radiation, as a covariable that has rarely been included in modelling dung decay.

## Methods

### Study site and field methods

Dung piles were monitored around Mbeli Bai, a large swampy forest clearing ('bai' in the local language) in the south-west of Nouabalé-Ndoki National Park, Republic of Congo (fig. 1). Fresh dung piles (maximum 24 hours old) were surveyed from shortly after deposition up to the day when we could not detect the dung from a distance of 2 m in the undergrowth (Barnes and Jensen (1987) stage E or Hedges and Lawson (2006) stage S4). Instead of monitoring a dung pile every 7 or 14 days until it decays (Barnes et al. 1997; Nchanji and Plumptre 2001), both authors monitored dung piles that were deposited 1) on the 2.6-km forest path from the research camp to the bai each day (bai path sample) and 2) on phenology trails (around 15 km) in the middle of each month (phenology path sample).

To calculate the lifespan of each dung pile, we calculated the number of days from date of first observation to date last seen in stage D, following morphological categories of Barnes and Jensen (1987).

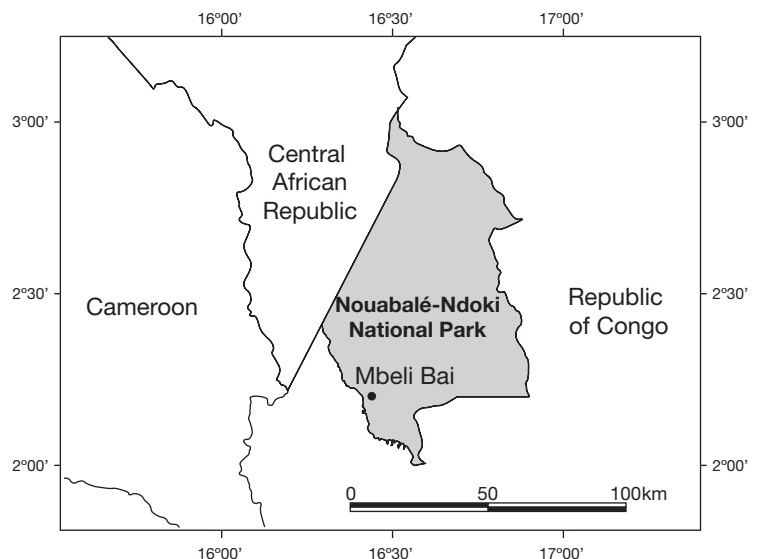


Figure 1. Location of Mbeli Bai in Nouabalé-Ndoki National Park. Map courtesy of Emma J. Stokes.

For dung piles encountered on the phenology path we added a random number between 0 and 30 to the time of deposition to last observation. To reduce the degree of subjectivity in deciding when a dung pile disappeared (see also Nchanji and Plumptre 2001) we monitored various dung piles before we started data collection to arrive at a certain consistency in deciding when a dung pile is no longer visible (Barnes 1996). Whenever we assigned different dates of disappearance of dung piles we used the midpoint of the dates we had assigned. We excluded dung piles that were deposited right on the path because other researchers, porters and trackers used the path and the dung decay there might not be as representative as from elsewhere in the forest (White 1995).

### Environmental covariables

We analysed habitat type and climatic factors such as rainfall, temperature and sunshine hours, which might influence the lifespan of elephant dung piles at our site. We did not systematically collect information on other factors such as canopy coverage, activity of other animals or leaf litter, which could potentially influence dung decay.

Three main habitat types can be distinguished in the study area: 1) monodominant *Gilbertiodendron dewevreii* (hereafter called *Gilbertiodendron* forest)—34% of study area with 66% closed canopy coverage; 2) mixed-species forest (mixed forest) on terra firma soil—62% of study area with 49% closed canopy coverage; and 3) seasonally inundated or swamp forest (inundated forest), often found along river courses—4% of study area with 41% closed canopy coverage. We recorded rainfall and temperature (daily maximum and minimum) at our research camp. We estimated solar radiation by monitoring sunshine hours during daily monitoring at the forest clearing. Rainfall variables used included rainfall of the date of deposition and the following 3 (R + 3), 10 (R + 10), and 30 (R + 30) days as well as rainfall of the 3 (R - 3), 10 (R - 10) and 30 (R - 30) days before deposition (Nchanji and Plumptre 2001). We followed the same process with sunshine hours after first detection of dung piles (S + 3; S + 10; S + 30); mean minimum daily temperature (MinTemp + 3; MinTemp + 10; MinTemp + 30); and mean maximum daily temperature (MaxTemp + 3; MaxTemp + 10; MaxTemp + 30) in the days after deposition. We did not aim to investigate how covariables associate with mean monthly dung dura-

tion (pooled dung piles monitored in the same month) because of the small monthly sample size ( $5.94 \pm 5.48$  piles/month, range 1–23).

### Statistical analysis

Previously multiple regressions have been employed to investigate the influence of various covariables on dung survival (Nchanji and Plumptre 2001). More recently Barnes et al. (2006) used a survival model (e.g. Cox hazard model) to evaluate the effect of covariables that had the greatest influence on dung survival. We adopted this approach; details of the method are given elsewhere (Cox 1972; Barnes et al. 2006). Given the large number of covariables, we first condensed variables by applying a principal component analysis (PCA) on each set of variables (rainfall, sunshine, maximum temperature, minimum temperature). Each PCA resulted in condensing three variables into one value with high correlation of the variables (mean 0.89, minimum 0.782). Following Barnes et al. (2006), we first fitted each independent variable by itself. We then added variables to the null model and retained the variables that produced the greatest reduction in  $-2\log L$ ; we continued this until no further significant reduction of  $-2\log L$  resulted. Models with AIC (Akaike Information Criterion =  $-2\log L * 2df$ ) of less than 2 are similar (Burnham and Anderson 2002).

### Results

We monitored 171 dung piles deposited from December 2002 to February 2006 on the forest path and 37 from November 2002 to August 2004 on the phenology trail (table 1). Sixty-two per cent of phenology trail dung piles ( $n = 23$ ) were encountered in mixed forest (11% in *Gilbertiodendron* forest, 27% in inundated forest); in the bai path sample only a minor portion of dung piles was encountered in mixed forest because most of the bai path covered monodominant *Gilbertiodendron* forest (54% in *Gilbertiodendron* forest, 15% in mixed forest, 31% in inundated forest). The survival of dung piles showed high variation with some piles disappearing within a couple of days and a few lasting several months. However, most dung piles quickly passed stage A, B and C within one or two days and then remained visible for a much longer period in stage D. The mean survival of dung piles in the bai path sample was  $51.3 \pm 36.8$  days (mean  $\pm$  SD; range 5–236) and in the phenology trail sample

Table 1. Summary of elephant dung decay duration revealed by the two different sampling methods and habitat types

Method / Habitat type	Sample size (n)	Minimum decay rate (days)	Maximum decay rate (days)	Mean decay rate (days)	Standard deviation
<b>Bai path sample</b>					
All	171	5	236	51.298	36.766
<i>Gilbertiodendron</i> forest	93	5	236	53.065	4.496
Mixed forest	25	10	112	57.600	5.895
Inundated forest	53	7	125	45.226	3.448
<b>Phenology path sample</b>					
All	37	3	168	65.243	40.321
<i>Gilbertiodendron</i> forest	4	53	93	78.500	8.770
Mixed forest	23	13	168	81.261	7.334
Inundated forest	10	3	74	23.100	8.182

65.2 ± 40.3 days (range 3–168). Although there was no significant difference in dung survival between the two sampling methods ( $t = -1.514$ ,  $P = 0.137$ ; data square root transformed), survival curves differed between methods (figs. 2a, 2c) and we therefore decided not to pool the data sets.

Dung decay of piles in the phenology path sample showed a slower rate of disappearance in the first 70 days with 57% of dung piles surviving to this age compared with only 22% of piles surveyed daily on the bai path. For both methods dung encountered in mixed forest survived longest (bai path sample: 57.6 days ± 29.5; phenology path sample: 81.3 ± 35.2) and dung in inundated forest disappeared quickest (bai path sample: 45.2 ± 25.1; phenology path sample: 23.1 ± 25.9) with dung found in monodominant *Gilbertiodendron* forest being intermediate (bai path sample: 53.1 ± 43.4; phenology path sample: 78.5 ± 17.5). Figures 2b and 2d show habitat-related differences in dung survival.

### Covariables

Given the small sample size of dung piles surveyed along the phenology trail and the different sampling period, we decided to limit all further analysis to the bai path sample of 171 dung piles. Survival of dung deposited in the dry-season months (less than 100 mm rainfall) ( $n = 95$ ) was 63.2 ± 37.5 days (range 13–236) and significantly longer compared with dung deposited in rainy-season months 41.6 ± 33.3 days (range 5–181) ( $t = 3.939$ ,  $P < 0.001$ ).

When we included each of the explanatory variables independently to the null model only the models

with ‘PC\_rain before’, ‘PC\_sun’, and ‘PC\_min\_temp’ remained significant, but not ‘PC\_rain after’ or habitat type; ‘PC\_max\_temp’ showed a trend (table 2). The ‘PC\_sun’ variable was retained because it was the best predictor of hazard (AIC = 1410.77).

The next model included ‘PC\_min\_temp’ (AIC = 1396.31). Including ‘PC\_rain before’ did not significantly improve the model (AIC = 1398.26).

The overall model, including all five principal components (PC) and habitat type as a categorical covariable, explained significantly the dung duration (AIC 1395.84, table 2). In this overall model only ‘PC\_sun’, ‘PC\_min\_temp’ and ‘PC\_max\_temp’ remained significant but not ‘PC\_rain before’, ‘PC\_rain after’, or habitat type.

Therefore, more sunshine and warmer daily minimum temperature appeared to cause longer dung survival whereas rainfall before deposition had no influence on dung duration in combination with sunshine and temperature.

When pooling monthly samples it appeared that mean monthly decay varied substantially between months up to a factor of 2.8 (fastest decay in September, 28 days; slowest decay in February, 79 days). Dung decay was fastest in August to October and slowest in February and March; it remained relatively constant between May and July (fig. 3).

### Discussion

Our preliminary data suggest that elephant dung-pile duration at Mbeli Bai is similar to that in data obtained in Lopé National Park (White 1995) and Makokou

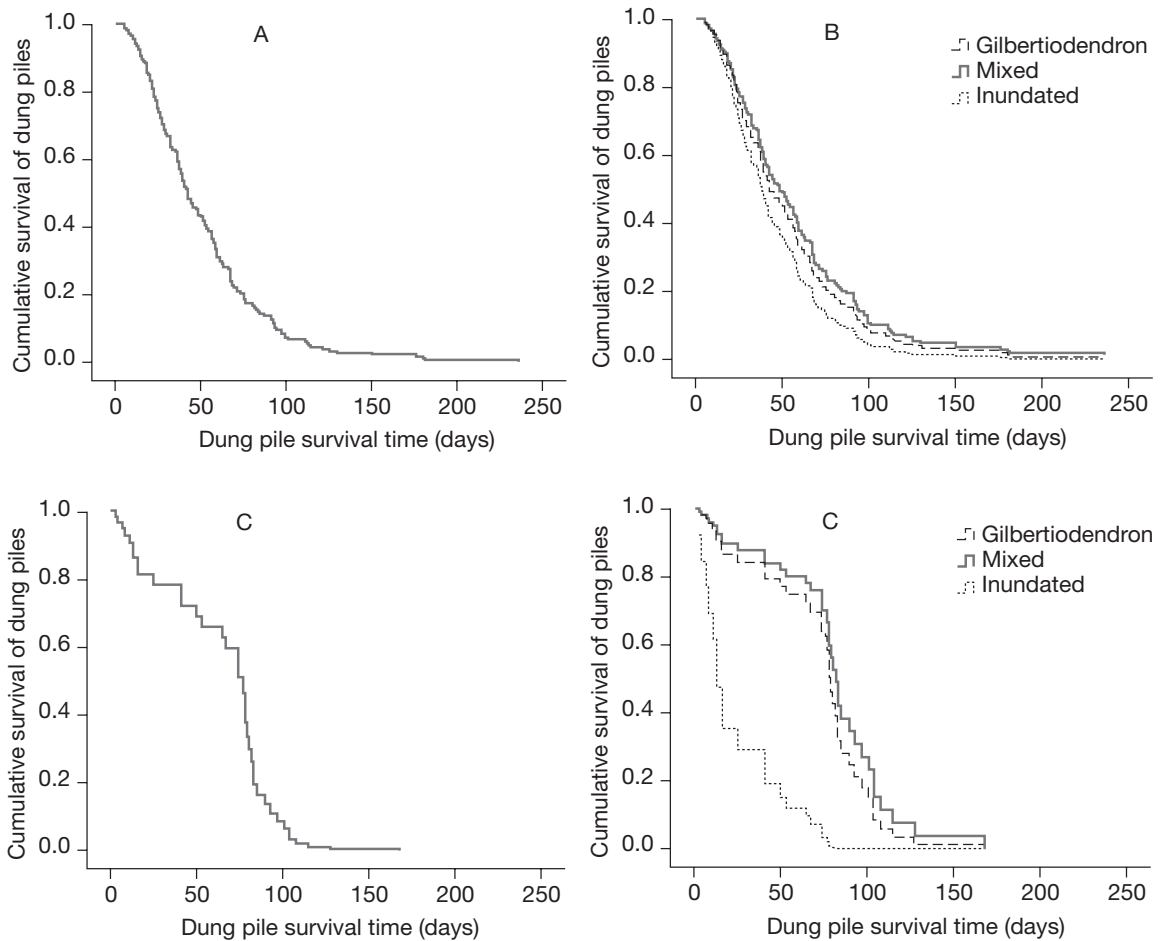


Figure 2. Cumulative survival plots of elephant dung piles showing A) all dung piles monitored on the bai path sample, B) habitat-specific curves of the bai path sample, C) all dung piles monitored on the phenology path sample, and D) habitat-specific curves of the phenology path sample.

in Gabon (Barnes and Barnes 1992) and in Virunga National Park, Democratic Republic of Congo (Mubalama and Sikubwabo 2002) but much shorter than dung decay rates obtained in Cameroon (Nchanji and Plumtre 2001). However, any dung survey ideally has to include a retrospective method prior to the survey (Hedges and Lawson 2006).

Our results confirm that there is substantial variation in dung survival even when dung piles are deposited under apparently similar subjective conditions (same habitat type, same day). Dung decay is a complex process that includes interaction of various environmental variables and hence it is not surprising to find that different studies have found different interactions with dung survival. In comparison with results from other sites

(Barnes and Barnes 1992; Barnes et al. 1997) the rate of disappearance after deposition (at least for the bai path sample) was very fast. Fresh dung piles quickly decayed and dung boli broke apart after a few days only (class D). Contrasting modes of disappearance can be caused by different decay of some dung components (fibre, leaf fragments, fruits, other faecal matter). Further studies monitoring different dung-pile classes and dung components through time could provide important insights on why the patterns of disappearance at our site differ. One possible explanation to this quick disappearance might be the increased activity of dung beetles and the absence of dung-pile baking under exposed sunlight. Dung beetles quickly remove the faecal matter of the dung pile and we could observe them causing the complete decay

Table 2. Results from a model using each of the five predictor variables separately and the overall hazard model

Variable in models	Unstandardized regression coefficient (B)	Standard error of B (SE)	Wald test significance value	Degrees of freedom (df)	Significance (p-values)	Expected beta (upper-lower 95% confidence interval)	Akaike Information Criteria (AIC)
Using each of the five predictor variables separately							
PC_rain_before	0.201	0.071	7.938	1	<b>0.005</b>	1.222 (1.063–1.405)	1422.25
PC_rain_after	0.021	0.068	0.092	1	0.762	1.021 (0.893–1.167)	1429.49
PC_sun	-0.369	0.086	18.394	1	< <b>0.001</b>	0.691 (0.584–0.814)	1410.77
PC_min_temp	-0.224	0.068	10.763	1	<b>0.001</b>	0.799 (0.699–0.914)	1419.64
PC_max_temp	-0.127	0.076	2.789	1	0.095	0.880 (0.758–1.022)	1426.70
Habitatcode			2.877	2	0.237		1428.76
Habitatcode(1)	-0.248	0.177	1.967	1	0.161	0.780 (0.552–1.104)	
Habitatcode(2)	-0.362	0.244	2.199	1	0.138	0.696 (0.431–1.124)	
Overall hazard model (AIC = 1395.84, $\chi^2 = 45.358$ , $P < 0.001$ , $df = 7$ )							
Habitat_code			4.119	2	0.128		
Habitat_code(1)	-0.343	0.186	3.400	1	0.065	0.709 (0.493–1.022)	
Habitat_code(2)	-0.446	0.269	2.740	1	0.098	0.640 (0.378–1.085)	
PC_rain_before	-0.035	0.090	0.153	1	0.696	0.966 (0.810–1.151)	
PC_rain_after	-0.055	0.087	0.401	1	0.527	0.947 (0.799–1.122)	
PC_sun	-0.581	0.120	23.396	1	≤ <b>0.001</b>	0.559 (0.442–0.708)	
PC_min_temp	-0.483	0.105	21.304	1	≤ <b>0.001</b>	0.617 (0.502–0.757)	
PC_max_temp	0.268	0.112	5.731	1	<b>0.017</b>	1.307 (1.050–1.627)	

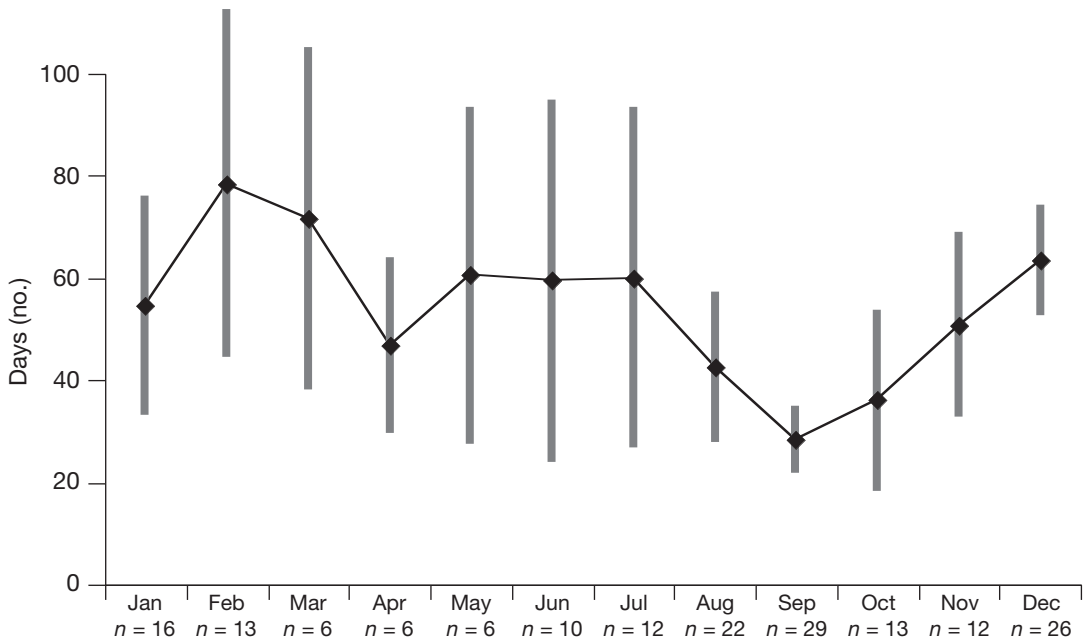


Figure 3. Mean monthly dung decay rates with  $\pm$  95% confidence limits ( $n$  – no. of samples).

of dung piles of western gorillas (*Gorilla gorilla*) and duikers (*Cephalophus* spp.) within a few hours. Other studies have shown that age is an important covariable that has to be included in any decay model (Laing et al. 2003; Kuehl et al. in press).

To our surprise, our findings do not confirm rainfall after deposition as being the most important factor influencing elephant dung decay as previously suggested (White 1995; Barnes et al. 1997; Nchanji and Plumptre 2001), although rainfall before deposition correlated with dung duration in the 0-model, showing that wet conditions on the date of deposition appear to have a positive effect on dung duration.

We found that increased sunshine slowed down the decay process. Sunshine has rarely been considered as a necessary covariable to include, possibly due to the effort needed in collecting data. However, many studies have clearly shown that sunshine can have a pronounced effect on dung survival by baking dung piles, which become 'fossilized' and remain visible for a long period (White 1995; Nchanji and Plumptre 2001). This effect is further supported by the fact that dung piles in more open forest and lower canopy coverage last longer (Nchanji and Plumptre 2001; Barnes et al. 2006). Our results appear to support this finding because dung piles lasted slightly longer in the mixed forest (with less canopy coverage) than in the *Gilbertiodendron* forest.

Further, sunshine might indirectly influence the activity of dung beetles, the main decomposers, through its negative effect on humidity, because sunshine is responsible for the decrease in humidity in Ndoki Forest (H.S. Kuehl, pers. comm.). Humidity triggers the emergence and onset of activity in dung beetles (Doube 1991) and possibly fungi (Masunga et al. 2006). Accordingly, termite and dung beetle activity appears to be less common in the dry season (White 1995) and in open habitats (Horgan 2005; Vernes et al. 2005).

Although we did not note other potential influential variables, it is plausible to assume that canopy coverage, elephant diet and activity of other seed consumers all influence dung duration. Given that fruit consumption of forest elephants is strongly seasonal (White et al. 1993; Blake 2002) it is plausible to assume that large mammals such as red river hogs (*Potamochoerus porcus*) adjust their seed consumption accordingly (White 1995). Observations from Mbeli Bai indicate that seed consumption from dung is more frequent during frugivorous months (T. Breuer pers. obs.). This activity

combined with the less fibrous diet during frugivorous months can further accelerate dung decay (White 1995, but see Nchanji and Plumptre 2001).

Additionally, in the semi-deciduous Ndoki Forest, leaf litter in the dry season appears to be higher than in the wet season. It was not uncommon to find elephant dung completely covered by old leaves. We also found that warmer daily minimum temperature resulted in longer dung survival, demonstrating that temperature is an important covariable that needs to be included in dung survival models. In contrast to White's (1995) finding that wet substrate slows down the decay process we found that dung deposited in swamp habitat decayed faster than on terra firma forest, possibly because many piles were washed away and the positive effect of sun baking was missing in these habitat types.

## Conclusion

Our study suggests that sunshine plays an important role in the complex process of elephant dung decay, and data on irradiance should therefore be included in modelling dung decay. Calculating cloud cover from satellite images can alternatively be used to estimate solar radiation. Given that many different factors influence dung survival we do not suggest extrapolating dung decay and instead support conducting site-specific dung decay experiments, which should take place before and during the dung survey. However, given the numerous factors that influence the decay process, monitoring an adequate number of dung piles can be time consuming and costly, particularly at sites of low density (Kuehl et al. in press). Our study also shows that adequate sampling in different habitat types including different canopy coverage is important. That might be particularly important given the longer survival of dung deposited in more open forest, potentially leading to an overestimation of elephant numbers in logged forests with disturbed canopy coverage. Further studies are needed to better understand the complex interaction of various climatic factors on dung decay, for example using the retrospective dung decay method (Laing et al. 2003). Using objective criteria of dung decay, such as dung height and volume, should be tested to reduce the degree of subjectivity in deciding when a dung pile disappears (Kuehl et al. in press). Alternative methods such as genetic capture-mark recaptures estimates (Eggert et al. 2003) or acoustic monitoring (Payne et

al. 2003) should be combined with dung estimates to improve our ability and precision to detect population changes.

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## References

- Barnes RFW. 1996. Estimating forest elephant abundance by dung counts. In: Kangwana K, ed., *Studying elephants*. AWF Technical Handbook no. 7. African Wildlife Foundation, Nairobi. p. 33–48.
- Barnes RFW, Asamoah-Boateng B, Naada Majam J, Agyei-Ohemeng J. 1997. Rainfall and the population dynamics of elephant dung piles in the forests of southern Ghana. *African Journal of Ecology* 35:39–52.
- Barnes RFW, Barnes KL. 1992. Estimating decay rates of elephant dung piles in forest. *African Journal of Ecology* 30:316–321.
- Barnes RFW, Dunn A. 2002. Estimating forest elephant density in Sapou National Park (Liberia) with a rainfall model. *African Journal of Ecology* 40:159–163.
- Barnes RFW, Jensen K. 1987. How to count elephants in forests. *IUCN African Elephant and Rhino Specialist Group Technical Bulletin* 1:1–6.
- Barnes RFW, Majam JN, Asamoah-Boateng B, Agyei-Ohemeng J. 2006. The survival of elephant dung piles in relation to forest canopy and slope in southern Ghana. *Pachyderm* 41:37–43.
- Blake S. 2002. The ecology of forest elephant distribution and its implications for conservation. PhD thesis. Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh.
- Blake S, Strindberg S, Boudjan P, Makombo C, Bila-Isia I, Ilambu O, Grossmann F, Bene-Bene L, de Semboli B, Mbenzo V, S'hwa D, Bayogo R, Williamson L, Fay M, Hart J, Maisels F. 2007. Forest elephant crisis in the Congo. *PLoS Biology* 5(4):111.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodal inference*, 2nd ed. Springer Verlag, Berlin.
- [CARPE] Central African Regional Program for the Environment (USAID). 2007. The forests of the Congo Basin: state of the forest 2006. CARPE. Unpublished report.
- Cox DR. 1972. Regression models and life-tables. *Journal of the Royal Statistical Society, Series B: Statistical Methodology* 34:187–220.
- Doube BM. 1991. Dung beetles of southern Africa. In: I. Hanski I, Cambefort Y., eds., *Dung beetle ecology*. Princeton University Press, Princeton, NJ. p. 133–155.
- Eggert LS, Eggert JA, Woodruff DS. 2003. Estimating population sizes for elusive animals: the forest elephants of Kakum National Park, Ghana. *Molecular Ecology* 12:1389–1402.
- Hedges S, Lawson D. 2006. *Dung survey standards for the MIKE Programme*. CITES MIKE Programme, Nairobi.
- Horgan FG. 2005. Effects of deforestation on diversity, biomass and function of dung beetles on the eastern slopes of the Peruvian Andes. *Forest Ecology and Management* 216:117–133.
- Inkamba Nkulu C. 2005. Suivi des baies et identification de l'éléphant de forêt (*Loxodonta africana cyclotis* Matschie, 1900) dans le Parc National de Nouabalé-Ndoki. Wildlife Conservation Society, Brazzaville. Unpublished report.
- Kuehl HS, Todd L, Boesch C, Walsh PD. In press. Manipulating decay time for efficient large mammal density estimation: goillas and dung height. *Ecological Applications*.
- Laing SE, Buckland ST, Burn RW, Lambie D, Amphlett A. 2003. Dung and nest surveys: estimating decay rates. *Journal of Applied Ecology* 40:1102–1111.
- Masunga GS, Andresen O, Taylor JE, Dhillion SS. 2006. Elephant dung decomposition and coprophilous fungi in two habitats of semi-arid Botswana. *Mycological Research* 110:1214–1226.
- Merz G. 1986. Counting elephants *Loxodonta africana cyclotis* in tropical rainforests with particular reference to the Tai National Park, Ivory Coast. *African Journal of Ecology* 24:61–68.
- Mubalama L, Sikubwabo C. 2002. Rate of decay of elephant dung in the central sector of Parc National des Virunga, Democratic Republic of Congo. *Pachyderm* 33:43–49.



- Nchanji AC, Plumptre AJ. 2001. Seasonality in elephant dung decay and implications for censusing and population monitoring in south-western Cameroon. *African Journal of Ecology* 39:24–32.
- Payne KB, Thompson M, Kramer L. 2003. Elephant calling patterns as indicators of group size and composition: the basic for an acoustic monitoring system. *African Journal of Ecology* 41:99–107.
- Plumptre AJ. 2000. Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology* 37:356–368.
- Turkalo A, Fay JM. 2001. Forest elephant behaviour and ecology: observations from the Dzanga Saline. In: Weber W, White L, Vedder A, Naughton L, eds., *Conservation and ecology of the African rain forest*. Yale University Press, Ithaca, NY. p. 207–213.
- Vanleeuwe H, Cajani S, Gautier-Hion A. 1998. Large mammals at forest clearings in the Odzala National Park, Congo. *Revue d'Ecologie : la Terre et la Vie* 53:171–180.
- Vernes K, Pope LC, Hill CJ, Barlocher F. 2005. Seasonality, dung specificity and competition in dung beetle assemblages in the Australian wet tropics, north-eastern Australia. *Journal of Tropical Ecology* 21:1–8.
- White LJT. 1995. Factors affecting the duration of elephant dung piles in rain forest in the Lope Reserve, Gabon. *African Journal of Ecology* 33:142–150.
- White LJT, Tutin, CEG, Fernandez, M. 1993. Group composition and diet of forest elephants *Loxodonta africana cyclotis* (Matschie, 1900) in the Lopé Reserve, Gabon. *African Journal of Ecology* 31:181–199.