Poaching empties critical Central African wilderness of forest elephants

By: John R. Poulsen, Sally E. Koerner, Sarah Moore, Vincent P. Medjibe, Stephen Blake, Connie J. Clark, Mark Ella Akou, Michael Fay, Amelia Meier, Joseph Okouyi, Cooper Rosin, and Lee J.T. White

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Abstract:

Elephant populations are in peril everywhere, but forest elephants in Central Africa have sustained alarming losses in the last decade [1]. Large, remote protected areas are thought to best safeguard forest elephants by supporting large populations buffered from habitat fragmentation, edge effects and human pressures. One such area, the Minkébé National Park (MNP), Gabon, was created chiefly for its reputation of harboring a large elephant population. MNP held the highest densities of elephants in Central Africa at the turn of the century, and was considered a critical sanctuary for forest elephants because of its relatively large size and isolation. We assessed population change in the park and its surroundings between 2004 and 2014. Using two independent modeling approaches, we estimated a 78–81% decline in elephant numbers over ten years — a loss of more than 25,000 elephants. While poaching occurs from within Gabon, cross-border poaching largely drove the precipitous drop in elephant numbers. With nearly 50% of forest elephants in Central Africa thought to reside in Gabon [1], their loss from the park is a considerable setback for the preservation of the species.

Keywords: Central Africa | forest elephants | poaching | Minkébé National Park, Gabon

Article:

Elephant populations are in peril everywhere, but forest elephants in Central Africa have sustained alarming losses in the last decade [1]. Large, remote protected areas are thought to best safeguard forest elephants by supporting large populations buffered from habitat fragmentation, edge effects and human pressures. One such area, the Minkébé National Park (MNP), Gabon, was created chiefly for its reputation of harboring a large elephant population. MNP held the highest densities of elephants in Central Africa at the turn of the century, and was considered a critical sanctuary for forest elephants because of its relatively large size and isolation. We assessed population change in the park and its surroundings between 2004 and 2014. Using two independent modeling approaches, we estimated a 78–81% decline in elephant numbers over ten

years — a loss of more than 25,000 elephants. While poaching occurs from within Gabon, cross-border poaching largely drove the precipitous drop in elephant numbers. With nearly 50% of forest elephants in Central Africa thought to reside in Gabon [1], their loss from the park is a considerable setback for the preservation of the species.

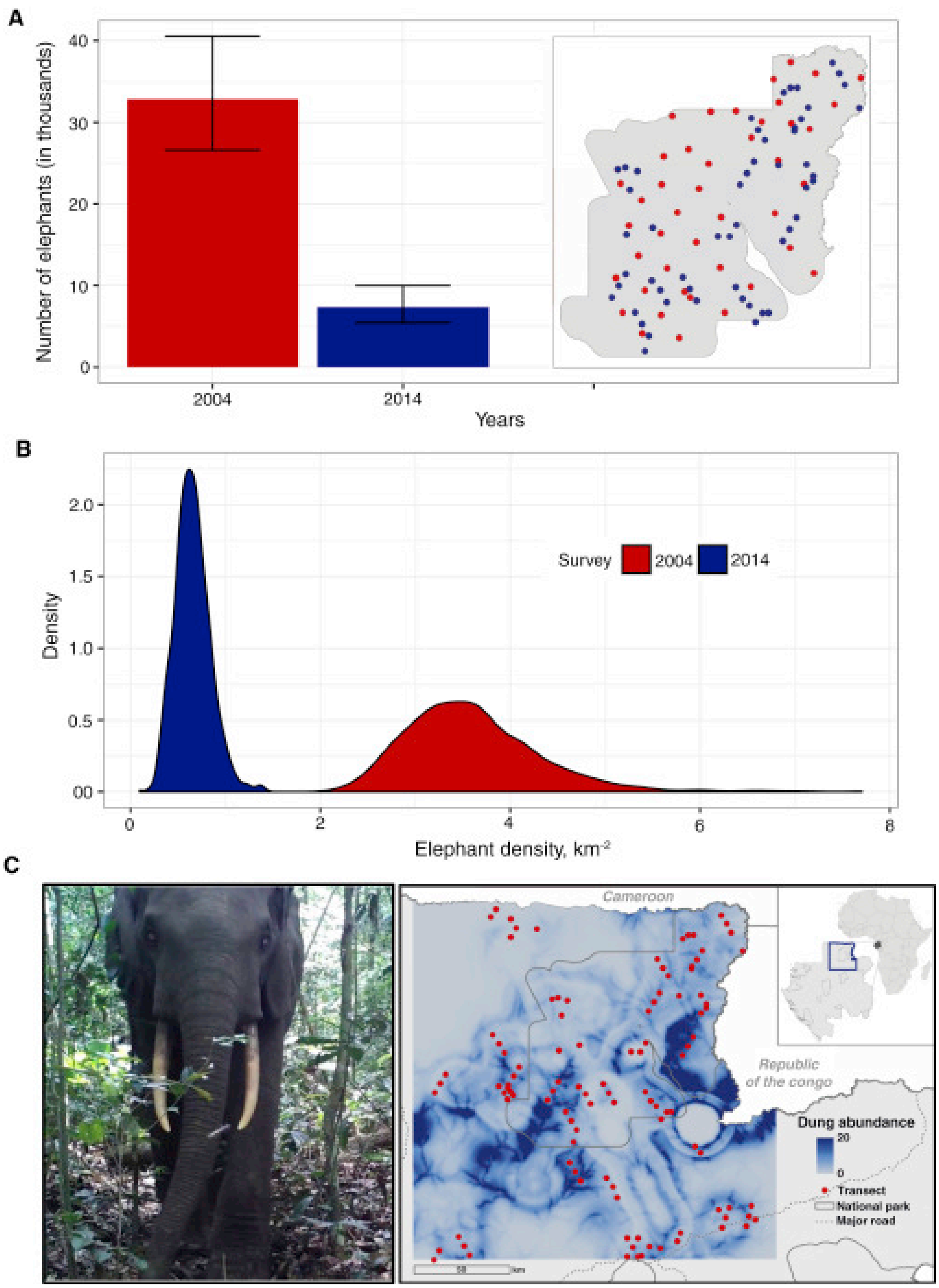

Figure 1. Forest elephants in Minkébé National Park, Gabon.
We estimated forest elephant numbers in the Minkébé National Park, Gabon (including a 5-km buffer zone) from 643 dung piles observed along 43 transects (43 km) in 2004 and 919 dung piles observed along 106 transects (199 km) in 2014. (A) Number of forest elephants (and 95% confidence intervals) in 2004 and 2014 estimated with

distance sampling, and (inset) the location of survey transects. (B) The bootstrapped densities of forest elephants for both survey periods from the dung-rainfall model. Note that the dung-rainfall model makes no assumption of steady-state dung decay; thus, unlike previous studies [1] declines in numbers are unambiguously attributable to real losses of elephants and not changes in precipitation regimes or other environmental variables (Supplemental information). (C) Forest elephant distribution map in 2014. The abundance of forest elephant dung was predicted across the study area using a density surface model. Dark blue indicates areas of high abundance, and the red points represent transects from the 2014 survey. Hotspots of high elephant density occur in the southeast corner of the park — far from villages and the Cameroon border — and the southwest corner of the park extending into the periphery zone. Areas of extremely low dung abundance occur in the northern portion of the study area abutting Cameroon, the southern portion of the study area near the Gabonese national road, and along a corridor through the park that coincides with the Ivindo River. From the model, we estimate 20,227 elephants in the study region with 7,206 elephants inside the park (Supplemental information): these estimates are within 2.2% of distance sampling results and 10.0% of dung-rainfall results. The inset shows the location of the study area in Africa and in Gabon.

Change in the elephant population was determined by comparing data from two large-scale surveys of elephant dung from 2004 to 2014. To ensure that the observed decline was not an artefact of different rainfall regimes between survey periods, we employed both the conventional distance-sampling method and a dung-rainfall model that makes no assumptions of steady-state dung decay (Supplemental information). With distance-sampling, we estimated a population in 2004 of 32,851 elephants in the park compared to just 7,370 elephants in 2014 (Figure 1A), a 77.6% decrease (Supplemental information). Similarly, with the dung-rainfall model, we estimated a population of 35,404 elephants in the park in 2004, compared to only 6,542 elephants in 2014, a loss of 81.5% of the population (Figure 1B).

The documentation of significant declines in forest elephant populations is not new 1, 2, but a 78–81% loss of elephants in a single decade from one of the largest, most remote protected areas in Central Africa is a startling warning that no place is safe from poaching. At 7570 km^2, MNP is the largest protected area in Gabon (34% larger than the average park in West and Central Africa) and lies 58 km from the nearest major national road. Strong evidence suggests that poaching is the cause of the precipitous drop in elephant numbers: ecoguards recorded 161 carcasses of poached elephants between 2012 and 2015; and much of the ivory seized on the international market has been traced back to the tri-national area of Cameroon, Gabon and Congo that includes MNP [3].

Our results suggest two fronts of poaching pressure on MNP (Supplemental information). Poaching from within Gabon reduced elephant numbers in the south of the park, whereas poaching from Cameroon emptied the northern and central sections of the park (Figure 1C). Declining dung abundance with distance from the park demonstrates that, while the park is under pressure, it is still buffered from Gabonese villages and cities that would be sources of poaching pressure from within the country. In the absence of effective law enforcement, timber concessions to the west and south of the park — accessible by logging roads — are easier poaching grounds than undisturbed forest [4]. But the strong, negative effect of the Cameroon border on elephant dung abundance suggests much of the poaching originated from Gabon's northern neighbor and emphasizes the importance of cross-border poaching. Cameroon's national road lies 6.1 km from MNP at its nearest point, making access to the park relatively easy. Cameroon plays a major role in ivory trade, with Douala serving as an important exit point for ivory [5]. In 2011, the National Parks Agency (ANPN) expelled over 6,000 illegal immigrants, mostly Cameroonians, from an illegal gold mining camp at the center of the park.

The site was a hub of criminal activities, including poaching, originating from the Cameroonian town of Djoum.

The government was unable to detect or stem the poaching of elephants for most of 2004–2014. Prior to 2011, the government invested little in park management: ANPN was under-resourced and under-staffed. Because of reports of poaching, the government raised the status of the forest elephant to 'fully protected', doubled ANPN's budget, and created the National Park Police. In 2012, Gabon became the first Central African country to burn its ivory stock. While laudable, these actions are clearly insufficient, as elephant poaching is an international problem driven by distant markets 5, 6 and facilitated by cross-border poaching. To save elephants, nations must cooperate by designing multinational protected areas, coordinating law enforcement, and prosecuting nationals who commit or encourage wildlife crimes in other countries.

At the CITES CoP17 in October 2016, efforts to list African elephants under Appendix 1 failed because of fears that some nations would pull out of all ivory trade restrictions. Similar reasoning prevented the IUCN African Elephant Specialist Group from recognizing the species. Our study supports listing forest elephants on CITES Appendix 1, and recognizing them as 'Critically Endangered' under the IUCN Red List. The international community must recognize the species to engender the multinational support necessary to prevent its extinction.

Author Contributions

Conceptualization, J.R.P., C.J.C., L.J.T.W., J.O., and M.F.; Methodology, J.R.P and V.P.M; Formal Analysis, J.R.P., S.M., C.R., A.M., and S.E.K.; Writing – Original Draft, J.R.P., S.M., and S.E.K.; Writing – Review & Editing, J.R.P., S.B., L.J.T.W., C.R., A.M., C.J.C., S.E.K, J.O., M.F.; Funding Acquisition, L.J.T.W., C.J.C., and M.F.; Supervision, J.R.P.

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Supplemental information
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Figure S1. Determinants of forest elephant abundance in 2014. The figures show the relationship between dung abundance and human pressures, including (A) the distance from the Cameroon border, (B) distance from Minkébé National Park, and (C) the number of human hunting sign. The blue shading represents 95% confidence intervals.

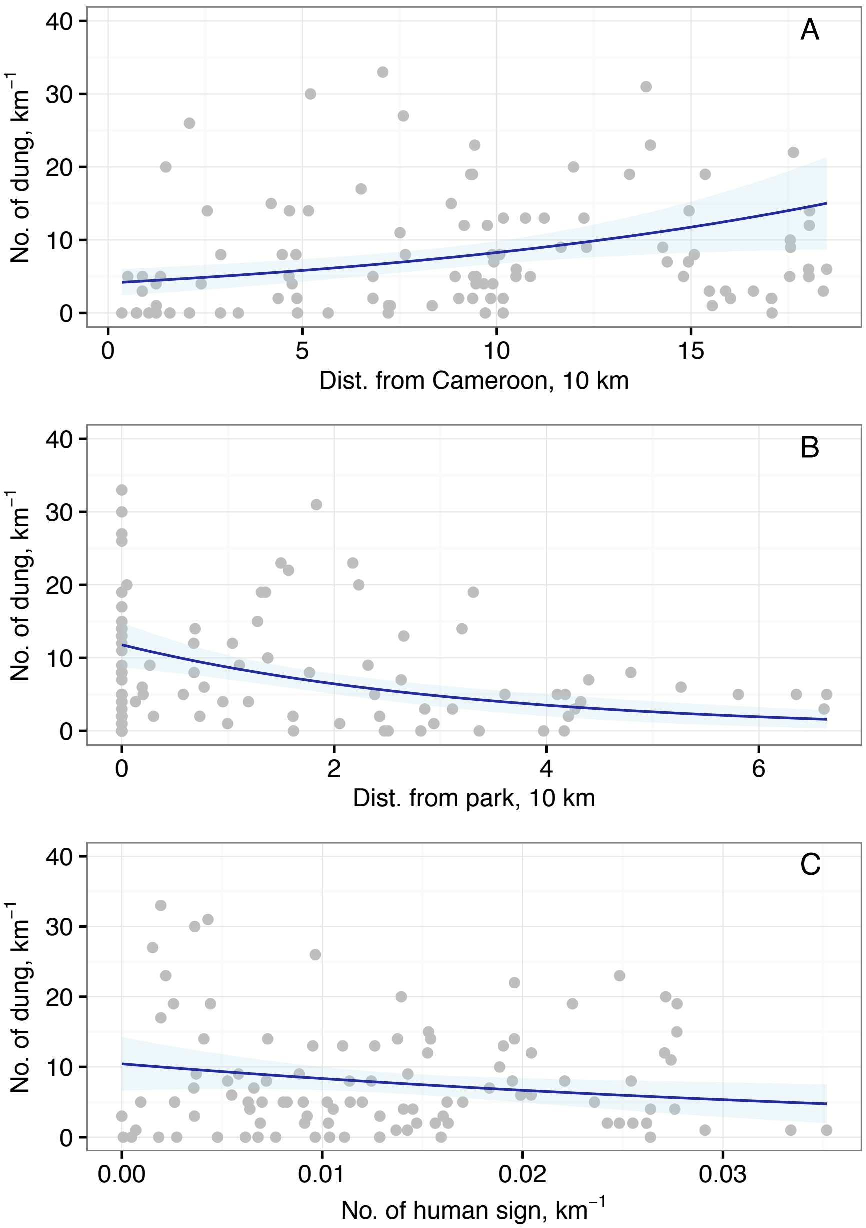

Table S1. Current (2014) and historic (2004) estimates of forest elephant density and abundance from distance analysis and a dung-rainfall model for three areas: 1) the entire landscape; 2) the Minkébé National Park; and, 3) the periphery of the park. Note that we only estimate the values for MNP in 2004. For each area, we show the density and abundance of elephants using three rates of dung defecation and decay time. Mean results from the dung-rainfall model are similar (within 12%) to the most conservative distance-based estimates of the forest elephant population calculated with a defecation rate of 19 dung piles per day and a dung decay rate of 90 days.

	Defecation rate (dung day^{-1})	Dung decay (days)	Estimated density (individuals km^2)			Estimated abundance (individuals)		
			Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI
Landscape (32,628 km^2) 2014	19.0	90.0	0.621	0.501	0.769	20,246	16,347	25,075
	18.1	45.5	1.291	1.042	1.598	42,108	34,000	52,151
	18.1	55.6	1.056	0.853	1.308	34,459	27,823	42,678
	dung-rainfall model		0.638	0.425	0.988	20,817	13,867	32,236
Minkébé NP (9,973 km^2) 2014	19.0	90.0	0.739	0.545	1.002	7,370	5,435	9,993
	18.1	45.5	1.537	1.133	2.084	15,328	11,304	20,783
	18.1	55.6	1.258	0.928	1.705	12,543	9,251	17,008
	dung-rainfall model		0.656	0.336	1.051	6,483	3,491	10,571
2004	19.0	90.0	3.294	2.669	4.065	32,851	26,618	40,540
	18.1	45.5	6.840	5.543	8.440	68,215	55,280	84,172
	18.1	55.6	5.597	4.536	6.907	55,819	45,238	68,884
	dung-rainfall model		3.550	2.530	5.100	35,404	25,232	50,862
Periphery (22,655 km^2) 2014	19.0	90.0	0.568	0.432	0.747	12,876	9,791	16,934
	18.1	45.5	1.182	0.899	1.555	26,781	20,364	35,220
	18.1	55.6	0.967	0.736	1.272	21,916	16,665	28,822
	dung-rainfall model		0.603	0.397	0.966	13,661	8,994	21,885

Supplemental Experimental Procedures

Site Description and Field Methods

Gabon and Minkébé National Park

Gabon is the second most forested tropical country in the world, with a near-zero deforestation rate and relatively low population density (6.5 people km^2; http://countrymeters.info/en/Gabon). Announced in 2002, the government created 13 national parks, setting aside 11% of the country's territory in 2007. The Minkébé National Park (7570 km^2) is the largest of these protected areas. The MNP is surrounded by a 5 km buffer zone, where hunting is prohibited but extractive industries are permitted following guidelines intended to avoid negative environmental impacts on the park. Logging concessions surround the park to the west and south, constituting a peripheral zone that extends to the national roads to the west and south. The Cameroonian and Congolese borders form the northern and eastern boundaries of the park – no cross-border buffer zones exist subjecting the park to poorly regulated industrial activities.

The MNP landscape is composed of Congolian lowland tropical forest, interspersed with inselberg forest, herbaceous swamps, and inundated river forest. With little spatial variation, the long-term (1990-2009) mean annual temperature of Gabon is 24.8°C, reaching a high of 25.9°C between January and March and a low of 22.8°C between June and August. Mean annual precipitation (MAP; 1700 mm) in northeastern Gabon is seasonal with a long dry season from June to August, a short dry season in January and February, and two wet seasons from March to May and October to December.

Forest elephant surveys

In 2014 and early 2015, we conducted a survey of forest elephants in MNP and its periphery as the first stage of a national elephant survey. We chose sampling sites using a systematic, random design in which we randomly selected sites within 50 x 50 km cells. At each sampling site, field technicians from the Parks Agency employed line transect sampling to survey elephants [S1], establishing three 2-km straight line transects with one central transect and two transects positioned 4 km to the northwest or southeast of the point at a bearing of 45º. The orientation of the transects varied with the watershed so that transects were walked perpendicular to the main river or road system to encompass possible gradients in animal densities. The field teams consisted of three technicians (two principal observers and a compass bearer) and 2-3 local guides, who walked slowly along the transects (0.5 – 0.75 km hr^{-1}) looking for observations. For each observation of elephant sign, the teams recorded: (a) the type of observation (direct observation, elephant dung, and elephant paths); (b) age of elephant dung (fresh, recent, old, very old); (c) signs of human activity (shotgun shells, campfires, machete cuts, elephant carcasses, etc.); (d) distance along the transect; and, (e) perpendicular distance between the transect and the center of the observation. The teams also recorded GPS points every 250 m along the transects, as well as the forest type (primary forest, secondary forest, savanna, flooded forest, swamp, gap).

Estimation of Elephant Densities with Distance-based Methods

For both the 2004 and 2014 datasets, we estimated elephant dung densities and calculated their associated coefficients of variation and 95% confidence intervals with Distance 6.2 [S2]. To ensure robust estimation of detection and an effective strip half-width – the strip extending on either side of the transect line such that as many dung are observed beyond the strip as are missed within it – we right-truncated the data to remove dung observations farthest from each transect [S1]. We fitted detection functions to the data sequentially with half-normal, uniform, and hazard-rate key functions combined with cosine, Hermite polynomial, and simple polynomial adjustment terms. The best model was selected on the basis of the lowest Akaike information criterion (AIC) score. We examined model fit with chi-square goodness-of-fit tests.

For 2014, we estimated elephant densities for two sets of dung data: (1) *2014 all dung*, including all age classes of dung observations (919 observations); and (2) *2014 recent dung,* excluding all dung from the oldest age class (very old dung = 128 observations). For both the 2014 all dung and 2014 recent dung datasets, the best model was the hazard rate with a cosine adjustment term; whereas the 2004 data were best modeled by the half-normal with no adjustment term. We converted dung densities and abundances calculated in Distance 6.2 to densities and abundances of elephants using three rates of dung defecation and decay time (Table S1).

For each area, we multiple the density by the total In the original analysis of the data, Blake et al. [S3] divided the park into strata of low and moderate human pressure, and reported densities of 3.8 and 2.9 elephants km^{-2} in each. Our estimate of elephant abundance for the park (Table S1) exceeds the original estimate of 22,678 elephants (95% CI = 16,882; 30,531) because we include the 5-km buffer zone in the total area surveyed.

Effect of Survey Design on Elephant Numbers

Although the 2004 and 2014 surveys employed the same methods, the survey designs differed and transects were not conducted in the same locations in the two time periods. To verify that the differences in survey designs were not responsible for the stark differences in forest elephant density and abundance, we analyzed the 2004 data using subsets of data that closely matched the 2014 transect locations. We did this in two different ways: Design A and Design B.

Design A: During the 2014 survey campaign, field teams could not access the north central portion of the park because of flooding of the river valley and surrounding swamps there, leaving a gap in the coverage of the park (Figure 1). Therefore, to evaluate the effect of this gap we used GIS to identify the 2004 transects conducted in the area, and remove them from the analysis. Ten transects and 267 observations were eliminated, leaving a total of 376 observations from 32 transects (32 km).

Design B: To make the survey designs as spatially similar as possible, we selected 2004 transects located within 10 km of the 2014 transects. Using GIS, we drew a 10 km circular buffer around each 2014 transect, and all 2004 transects that did not fall within this buffer were removed. Eleven transects and 236 observations were eliminated, resulting in a total of 407 observations from 31 transects (31 km).

We estimated density and abundance of forest elephants from both appended datasets as described in the Methods. For both datasets, we truncated the data at 2.5 m and binned the data in 0.25 m bins. This resulted in the removal of 8 observations (2%) for Design A and 23 observations (6%) for Design B. Both Design A and Design B were best modeled with uniform key function with cosine adjustment term. Neither of the estimates from the two designs were significantly different than the estimates from the full dataset (Full: density = 3.29 individuals km^{-2} (95% CI: 2.67, 4.07); Design A: density = 2.95 (95% CI: 2.45, 3.54); Design B: density = 1.30 (95% CI: 2.48, 3.72). Both alternate designs resulted in a non-significant decrease in mean elephant abundances compared to the full design (Design A = 11% lower; Design B = 8% lower). As Design A and B were not significantly different from the full design, we present the entire dataset in the main text.

Estimation of Elephant Densities with Dung-Rainfall Models

Surveys of forest elephant populations are often conducted by counting dung piles to obtain a measure of dung density. Estimates of dung density estimates are then converted to numbers of elephants. This is most commonly accomplished by dividing the dung density by values of dung deposition and decay rate from the literature. Assuming that dung decay is in a steady state – that the decay rate is constant over time – simplifies calculations, but may be invalid [S4]. In particular, dung pile density and survival duration have been shown to be negatively correlated with rainfall, which varies monthly and annually [S5, S6]. Failure to account for variation in precipitation, therefore, could lead to faulty conclusions in comparisons of elephant populations over time if changes in elephant numbers are due to differences in dung decay, rather than poaching or other drivers.

Here we evaluate whether the perceived decline in elephant densities from 2004 to 2014 is a real phenomenon or an artefact of differences in rainfall that could have altered dung decay rates between the surveys. To do so, we: (1) examine trends in precipitation in the Minkébé landscape between 2003 and 2016; (2) test for differences in rainfall between the 2004 and 2014 surveys; and, (3) develop a dung-rainfall model for the Minkébé area. The dung-rainfall model permits the estimation of elephant densities from monthly rainfall, without using dung decay rates from the literature and without assuming that dung decays is in a steady state.

Trends in precipitation

There are no active meteorological stations in the northeast of Gabon, and therefore we downloaded daily data from the TRMM (Tropical Rainfall Measuring Mission) dataset. The data set (TRMM 3B42RT) provides daily estimates of precipitation at the 0.25 x 0.25 degree scale. We used the NASA Simple Subset Wizard (http://disc.sci.gsfc.nasa.gov/SSW/#keywords=GLDAS_MOS10_M%20001,TRMM_3B42RT_Daily%207) to download the data for the Minkébé landscape, averaging across the area to get a single daily precipitation value. With these data, we plotted the monthly rainfall from 2003 to 2016. There was no significant trend in rainfall over the 13-year period ($F_{1,154}$ = 0.030, R^2 = -0.006, p = 0.8638).

We also used Seasonal Trend Decomposition using Loess (STL) to divide up the time series into three components, namely the trend, seasonality and remainder. STL demonstrates a clear seasonal pattern in rainfall, but a very weak trend: the trend moves between 130 and 170 mm of rain, which is less than the variation in monthly rainfall. The lack of a strong trend over time suggests that our elephant densities are at least not affected by a consistent temporal change in rainfall that could affect dung decomposition rates.

Differences in precipitation between 2004 and 2014

To specifically test differences in rainfall between the two survey periods, we compared monthly rainfall between the 2003-2004 period and the 2014-2015 period. We use two-year periods in each case because the rainfall preceding the actual dung surveys could affect the number of dung on the forest floor (see below). The monthly rainfall for each period was 137.4 mm (± 91.3) in 2003-2004 and 141.5 mm (± 117), with no significant difference in rainfall between the two periods (pair t-test, t = -0.243, df = 23, p = 0.809). Again, this provides evidence that there were not strong differences in precipitation that could affect dung decay rates between surveys.

Derivation of dung-rainfall model to estimate elephant densities

Both White [S6] and Barnes et al. [S5] demonstrated that rainfall affects elephant dung decay. White [S6] found that rainfall in the month of deposition plus the preceding two months best predicted dung decay rate in Gabon. Barnes et al. [S5] found dung density could be predicted by the rainfall in the two months preceding dung deposition in Ghana. Barnes et al. [S5] proposed a model for deriving elephant numbers based on precipitation, but cautioned that differences in the relationships between dung decay and environmental variables vary from one country to another.

We used Barnes et al.'s [S5] method to derive a model for northeastern Gabon (Minkébé landscape). The backbone of the method is to develop a model relating dung density to rainfall at a site with known elephant density. The resulting equation provides a conversion factor to translate dung density into elephant numbers without relying on rates of dung decay. To do this, we first use an independent dataset from the Makokou area, that includes the southern part of the Minkébé landscape, to derive the dung-precipitation model [S7]. We then apply the model to the 2004 and 2014 surveys to obtain elephant densities for both surveys that do not rely on the steady state assumption. Finally, we compare the modeled densities of elephants to estimates derived using traditional methods based on dung decay.

In an independent study, we quantified wildlife densities and abundances from 24 straight line transects walked monthly in 2014. This study occurred in the southern part of the Minkébé landscape, from the northern section of the Ivindo National Park to the logging concessions north of Makokou and National Road 3. Like the Minkébé landscape, the forest in this area is Congolian lowland tropical forest. Field teams made both direct observations of live animals and indirect observations of animal sign (dung, ape nests, etc.) over one year [S7]. From the direct observations of forest elephants, we estimated the density, E_d, to be 0.75 elephants km^{-2} [95% CI = 0.472, 1.056].

Following methods proposed by Barnes et al. [S5], we regressed the density of elephant dung piles with average monthly precipitation to derive a dung-precipitation model. We built several linear mixed models, with monthly dung density for the transects as the response variable, and rainfall during the month of deposition, M_{T0}, and the three previous months of rain, (M_{T-1}, M_{T-2}, M_{T-3}), as independent variables. Because transects were walked each month, we treated transect identity as a random effect. We used the Akaike Information Criterion (AIC) to compare models.

The two best-fitting models included a single independent variable: M_{T-2} or M_{T0}. These two models fit the data equally well (ΔAIC < 2). Below we model elephant abundances for the Minkébé landscape using only M_{T-2} (the model with the lowest AIC), as the results from both models were very similar.

From the dung-rainfall model,

$$\hat{Y}_m = 1697.1 - 1.023 x_{m-2} \#[1]$$

where $\hat{Y}_m$ is the expected dung km^{-2} for month, m, and x_{m-2} is the rainfall two months before the survey month, we estimated the density of dung expected with 0.75 elephants km^{-2}. For simplicity, we converted $\hat{Y}_m$ to the dung density assuming 1 elephant km^{-2} by multiplying each value of $\hat{Y}_m$ by $1/E_d$. Thus, with $\hat{Y}_m$ as the number of dung that would be found if there were 1 elephant km^{-2}, we converted the density of observed dung, Y_m, to the density of elephants per month, E_m, with:

$$E_m = Y_m\left(1/\hat{Y}_m\right) \#[2]$$

or

$$E_m = Y_m(C) \text{ where}$$
$$C = 1/\hat{Y}_m \#[3]$$
.

We applied the model to rainfall data for the survey periods in both 2004 and 2014 to obtain the density of elephants for each month in the survey periods, and then averaged E_m across months to get a single density estimate for both periods.

To estimate confidence intervals for E_m, we used a bootstrapping procedure that takes into account variance in C and Y_m [S8]. We first bootstrapped equation 1 to obtain 1000 estimates of $1/\hat{Y}_m$ or C for each survey month. We then bootstrapped Y_m 1000 times, allowing the number of observed dung piles to vary each month. Estimates of E_m were then obtained by multiplying the bootstrapped estimates of C by a bootstrapped estimate of Y_m, resulting in 1000 independent values of E_m (i.e. 1000 values for each month in both surveys). To derive a mean density of elephants for 2004 and 2014, we averaged the values of E_m for a single bootstrap, resulting in a distribution of 1000 estimates of E, the mean elephant density. The median of E and the 95 percentiles provided the overall estimate of E and its 95% confidence intervals.

We estimated the density of elephants in Minkébé National Park to be 3.55 elephants km^{-2} [95% CI: 2.53, 5.10] in 2004 and 0.65 [95% CI: 0.35, 1.06] elephants km^{-2} in 2014. These estimates are similar (within 15%) to those obtained using a dung decay rate of 90 days for both 2004 and 2014 (Table S1). The modeled 2004 estimate was 7% higher than the dung decay-based estimate, whereas the modeled 2014 estimate was 12.0% lower. The difference in densities between the two surveys was 2.89 elephants km^{-2} [95% CI: 2.01, 4.27], indicating that the elephant population in Minkébé NP has fallen by 81.4% and representing a loss of 21,877 elephants from the park.

Evaluating the Determinants of Elephant Dung Abundance

To evaluate the determinants of elephant dung abundance, we related counts of dung to fourteen explanatory variables: distances from the borders of Cameroon, Congo and Equatorial Guinea, distances from nearest village and major city (regional capitals with > 10,000 people), distances from nearest major and secondary (logging) roads, distances from nearest major rivers (Ivindo River) and any waterway, distance from MNP, as well as the number of elephant carcasses, number of human hunting sign, slope and elevation. For most of the independent variables, we used ArcGIS 10.3.1 to assign values to each transect using existing spatial information on infrastructure and environmental features (unpublished data, Agence Nationale des Parcs Nationaux; [S9]). All distances were calculated from the center of each transect to the nearest point of interest (e.g. major road, border, or village). Information on elephant carcasses was collected by the Gabon Parks Agency law enforcement teams between 2013 and 2015. Density of human sign was calculated from observations made by the field teams.

We examined potential anthropogenic and environmental drivers of dung abundance using both generalized linear (GLM) and generalized additive (GAM) models. In all cases, the GLM's fit the data as well as the GAM's, and therefore we only present the GLM results. Before building models, we first checked for multicollinearity among all potential explanatory variables, removing the variable from any pair of highly correlated variables ($|r| > 0.7$ [S10]) that had the lowest correlation with the response variable. We also included an offset to adjust for differences in transect lengths [S11]. We also evaluated whether the data were best fit with a Poisson distribution (variance ≈ mean), negative binomial distribution (dispersion parameter is fitted to account for overdispersal, variance >> mean data), or zero inflated models (count variables with excessive zeros and overdispersion). In all cases, models parameterized with the negative binomial distribution fit the data better than the other models; thus, we only present these results. All models were fit in R version 2.7.1 [S12].

In preliminary analyses, no single model clearly fit the data better than others, and stepwise model selection sometimes chose different models depending on the direction of the selection procedure [S13]. Therefore, we also averaged the models to reduce model selection bias and account for model selection uncertainty [S14]. We fitted models to all possible combinations of explanatory variables (i.e. 16,383 possible combinations for our 14 variables) and averaged models and parameters using the MUMIn package [S15]. We considered all models within 4 AIC as equally informative [S16], and assessed the importance of the explanatory variables by their frequency of occurrence in the models.

In the current MNP landscape, anthropogenic drivers, including human sign and distance from park and national borders, determine elephant dung abundance (Figure S1). Elephant dung abundance increased significantly with distance from the Cameroon border and decreased significantly with distance from MNP and the density of human sign. The negative relationship between dung abundance and human sign reinforces the notion that poaching is eradicating forest elephants. Declining dung abundance with distance from the park demonstrates that, while the park is under pressure, it is still buffered from Gabonese villages and cities that would be sources of poaching pressure from within the country. The strong, negative effect of the Cameroon border on elephant dung abundance suggests much of the poaching originated from Gabon's northern neighbor and emphasizes the importance of cross-border poaching.

Description of Density Surface Modeling.

We used density surface modeling (DSM) to predict densities of forest elephant dung across the study landscape. DSM models the density of a species (or species sign, like dung) by first estimating the density per segment using similar methods to the Distance analysis, including a detection function. Density estimates are then modeled across the landscape as a function of different environmental or anthropogenic covariates using generalized additive modeling (GAM).

We subdivided each of the transects into 90 m segments to reflect the spatial scale of the environmental and anthropogenic variables [S2]. With 24 potential variables, we used Random Forest (RF) to identify the variables that best determined the probability of dung presence for each 90-m segment. RF is a popular machine learning model commonly used for variable selection [S17]. To reduce multicollinearity, we first examined correlations between the 24 environmental variables (using $|r| > 0.7$ as a cut-off for multicollinearity; [S10]. For any pair of highly correlated variables, we retained the variable with the greatest mean decrease in accuracy in the Random Forest (RF) model. We then divided the data into 10 separate datasets with a 1-1 ratio of random segments with and without dung [S18]. For each dataset, RF built 500 classification trees and ensembled them into a final tree. The ten RF models were then averaged to create a final model and to calculate the relative importance of each candidate covariate. The variables retained from the final model were included in the modeling of elephant dung density using GAM's (see below).

Density surface modeling accounts for survey effort (i.e. distance surveyed), probability of detection, and the potentially non-linear relationship between environmental covariates and dung density. The equation takes the following form:

$$n_j = \hat{p}_j A_j \exp\left[\beta_0 + s_1\left(\beta_1 x_{1j}\right) + s_2\left(\beta_2 x_{2j}\right) + \cdots \; s_z\left(\beta_z x_{zj}\right) \right],$$

where n_j is the count distribution, $\hat{p}_j$ is the probability of detection and A_j is the segment area, calculated as two times the truncation distance and length of each segment. The rest of the model follows a traditional GAM where β_0 is the intercept and the sum of the smoothing functions (s) applied to each coefficient (β_z) of the predictor (x_{zj}).We modeled the distribution of dung counts per segment as a negative binomial with a log link function. The maximum basis dimension for each spline was set at 20 to ensure enough "room" for model fitting [S19].

We first built a full GAM model and then used backwards model selection to find the most parsimonious model, removing non-significant variables ($p > 0.10$). With the final, most parsimonious model, we calculated dung density across the landscape at a scale of 30m^2, so that the number of dung is estimated for every 30m^2 grid cell on the map. By adding the dung counts together, we can calculate a total dung abundance and visualize it across the landscape. All data analysis was conducted in R v.3.2.1, using the randomForest and dsm packages [S20, S21].

The final model explained 20.4% of the deviance in the data ($p < 0.05$) and included six significant variables: distance to village, distance to the Ivindo River, distance to Cameroon border, elevation, slope, and the density of human signs. The DSM estimated 20,227 elephants in the study region with 7,206 elephants inside the park. These modeled estimates are very similar (within 2.2%) to our estimates from the field data.

Supplemental References

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