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Towards standardisation of population estimates: defecation rates of elephants should be assessed using a rainfall model

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Daily defecation rate is an important variable in density estimation of African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants. However, there has been no attempt to construct a general model that predicts defecation rates. By comparing 16 published studies, we found that annual and seasonal daily defecation rates increased with annual rainfall following a power regression model. We recommend calculating defecation rates based on the regressions from our meta-analysis, rather than using a defecation rate from any single study.

Introduction

Daily defecation rates play an essential role in estimating the density of elephants (Barnes 2001), especially for African forest elephants (*Loxodonta africana cyclotis*) but also for African savannah elephants (*L. a. africana*) and Asian elephants (*Elephas maximus*). Most population estimates of elephants are based on three variables: (1) dung density, (2) dung decay rates, and (3) daily defecation rates (Barnes 2001). Dung density estimates can be standardised using distance sampling (Thomas *et al*. 2010). Dung decay rates have been assessed in several independent studies (*see* review in Olivier *et al*. 2009). Because these estimates vary widely, Barnes and Dunn (2002) used a rainfall model to overcome the problem of variable decay rates associated with differences in rainfall. However, daily defecation rates have not been standardised for calculating elephant density. Some studies used locally determined defecation rates (e.g. Merz 1986, Ekobo 1995, Theuerkauf *et al*. 2001), while others chose a particular defecation rate from another location (e.g. Barnes *et al*. 1997, Jefferson *et al*. 1997) or averaged rates across studies (Olivier *et al*. 2009). Instead of arbitrarily choosing a defecation rate from one or more studies, we believe that it would be better to model defecation rates based on all published data. Although several studies showed that defecation rates differ in the wet and dry seasons (Barnes 1982, Ruggiero 1992, Nchanji *et al*. 2008), no attempt has been made to assess the impact of rainfall on defecation rates. Understanding the influence of rainfall will help to standardise and improve the accuracy of elephant population estimates based on dung counts. To contribute to a standardisation in estimations of elephant populations, we assessed the relationship between annual and seasonal defecation rates and annual rainfall by a meta-analysis of published studies.

Methods

We reviewed the literature for studies on African and Asian elephant defecation rates (D). We found 16 studies (Table 1) that provided original data on daily defecation rates (number of dung piles produced by one elephant per day). If authors only provided seasonal defecation rates, we estimated the annual defecation rate as the mean between dry and wet seasons weighted by the length of each respective season. Because the accuracy of each single study depends on its sample size, for each study we used a specific weighting factor. We calculated the weighting factors as the number of days elephants were tracked in a given study divided by the mean number of days elephants were tracked across all studies, as described in detail in Theuerkauf and Ellenberg (2000). For calculating confidence intervals of elephant density estimates based on dung surveys (Barnes 1993), it is necessary to know the coefficient of variance ($CV = SE \times mean^{-1}$). We therefore provide equations that allow the calculation of the CV value for any given defecation rate ($CV = SE \times predicted\ value^{-1}$).

Although most studies provided information on annual rainfall (R), we used the WorldClim database (Hijmans *et al*. 2005) to obtain standardised means of annual rainfall (in mm). WorldClim is a set of global climate layers with a maximum spatial resolution of 30 arc-seconds (about 1 km^2). The data base provides local rainfall data from about 1950 to 2000, averaged over cells of approximately 18 × 18 km, or 10 arc-minutes (http://r-gis.org/climate/worldclim1_4/grid/cur/bio_10m_esri.zip). For each study, we averaged annual rainfall values (Table 1) over the study area (4–9 cells) with ArcGIS 9.3 (ESRI Inc.). We then used PASW Statistics 18 (SPSS Inc.) to calculate best fit regressions. Barnes (1993) suggested the use of monthly rainfall to model defecation rates. We used annual rainfall instead of monthly rainfall for two reasons. First, we think

Table 1. Mean annual rainfall estimated from the WordClim database (Hijmans *et al.* 2005), number of days elephants were followed, and annual and seasonal daily defecation rates drawn from 16 studies of African and Asian elephants.

Area and study	Rain (mm)	Days	Defecation rate		
			Annual	Dry	Wet
Kunene Region, northwest Namibia (Leggett 2008)	130	30	8.0	7.5	8.9
Sengwa Wildlife Research Area, Zimbabwe (Guy 1976)	680	15	12.2	11.8	12.6
Ruaha National Park, Tanzania (Barnes 1982)	685	8	15.1	9.6	31.7
Kasungu National Park, Malawi (Jachmann & Bell 1984)	832	6		15.7	
Nazinga Game Ranch, Burkina Faso (Jachmann 1991)	909	4	17.4	14.1	27.2
Rwenzori National Park, Uganda (Wyatt & Eltringham 1974)	949	16	11.3	11.3	11.3
Manovo-Gounda St. Floris National Park, Central African Republic (Ruggiero 1992)	964	25	14.4	12.2	16.6
Kibale Forest Reserve, Uganda (Wing & Buss 1970)	1195	17	17.0	15.9	17.3
Bossematié Forest Reserve, Ivory Coast (Theuerkauf & Ellenberg 2000)	1365	9	17.5	16.6	18.1
Birungas, Rwanda (Plumptre 2000)	1581	2	16.2	16.2	16.2
Lobeke Forest, Cameroon (Ekobo 1995)	1620	24	17.2	17.2	17.2
Tai National Park, Ivory Coast (Merz 1986)	1770	8	18.0	18.0	18.0
Mudumalai Wildlife Sanctuary, India (Santosh & Sukumar 1995)	1862	25	18.0	18.0	18.0
Way Kambas National Park, Sumatra (Hedges & Lawson 2006)	2148	142	18.1	18.1	18.1
Santchou Reserve, Cameroon (Tchamba 1992)	2206	129	19.8	19.8	19.8
Banyang-Mbo Wildlife Sanctuary, Cameroon (Nchanji *et al.* 2008)	2687	72	16.8*		

* only adult elephants considered (we did not use seasonal defecation rates for this study as the authors reported that they observed seasonal variation in defecation rates but did not provide seasonal values).

that mean annual rainfall is a better indicator of the general food availability in an ecosystem than monthly rainfall. This is because we expect that a month with say 100 mm of rainfall in a rainforest will not change the food availability as much as the same amount of rain in a savannah. Second, many studies did not state for which months they assessed defecation rates.

Results and discussion

Annual and seasonal daily defecation rates from the 16 studies increased with increasing annual rainfall and were best described by power models (Fig. 1). Defecation rates of Asian elephants fitted well the regression lines for African elephants, therefore, we pooled data of the two elephant species. Annual defecation rates can be estimated as $D_{annual} = 2.01R^{0.287}$ ($r^2 = 0.850$, $P < 0.001$). The coefficient of variance for each respective defecation rate would be $CV_{annual} = 0.74R^{-0.287}$. The predicted value for the annual mean defecation rate in a study area with 1000 mm of annual rainfall is 14.6 and its coefficient of variance 10.2%, while in an area with 3000 mm of annual rainfall the defecation rate is 20.0 with a CV of 7.4%. The correlation was even stronger for the dry season: $D_{dry} = 1.25R^{0.352}$ ($r^2 = 0.919$, $P < 0.001$) and $CV_{dry} = 0.87R^{-0.352}$. During the wet season, there is more variation in defecation rates, resulting in larger confidence bands: $D_{wet} = 2.79R^{0.25}$ ($r^2 = 0.630$, $P = 0.001$) and $CV_{wet} = 1.04R^{-0.25}$. The two studies that lay outside the confidence bands had very low sample sizes and, because of their resulting small weighting factors, had minimal influence on the model. Previously observed large differences in defecation rates during dry and wet seasons in savannahs (e.g. Barnes 1982, Jachmann 1991) can therefore be explained mostly by small sample size.

Nchanji *et al*. (2008) suggested that the higher defecation rates during wet seasons coincide with a higher availability of food. In fact, the number of species consumed and dispersed by elephants is proportional to monthly precipitation (Theuerkauf *et al*. 2000). Besides, seasonality usually becomes less pronounced as the annual rainfall increases. Mean annual rainfall can therefore be seen as a variable that represents seasonal variability in food availability. This results in asymptotic (power) functions of annual rainfall and defecation rate with little difference between seasons at large rainfall values. As a consequence, all three models of annual and seasonal defecation rates predicted a defecation rate of about 20 for regions with 3000 mm of annual rainfall. At low values of annual rainfall defecation rates were predicted to be lower in the dry season than in the wet season.

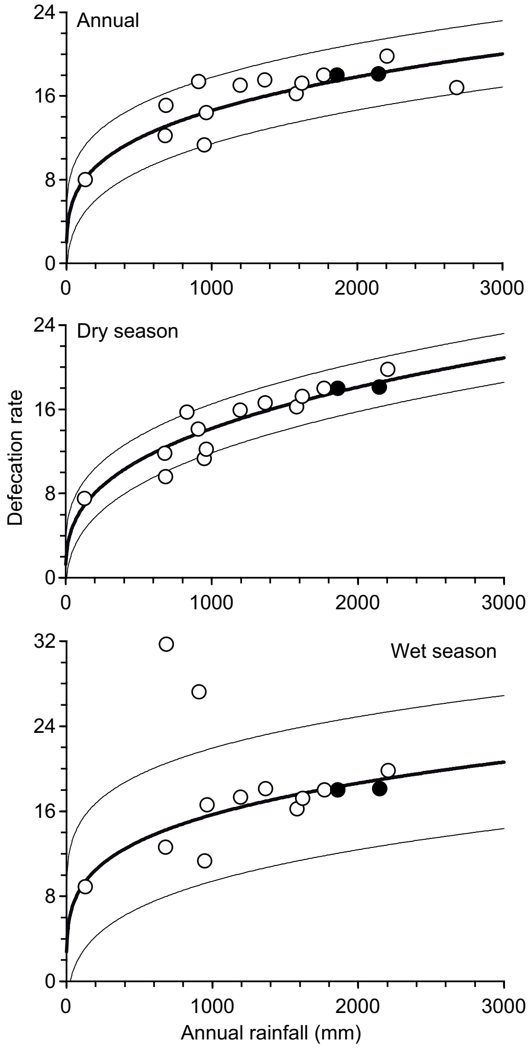

Fig. 1. Power regression lines (with 95% CIs) of the relationship between annual and seasonal daily defecation rates of African (empty circles) and Asian (filled circles) elephants and mean annual rainfall. The data were weighted by the number of days elephants were followed in each respective study (Table 1).

The strong relationship between mean annual rainfall and defecation rates suggests that it is inappropriate to calculate elephant densities from daily defecation rates that are arbitrarily selected or averaged across studies. The use of locally estimated defecation rates is an alternative, but single studies are limited by sample size. Deriving data from many studies provides more rigorous results (Johnson 2002) and the function between rainfall and defecation rate can be averaged. Therefore, we recommend that daily defecation rates are estimated using the regression functions from our meta-analysis and the global rainfall database. This would reduce bias in density calculations, and contribute to the standardisation of elephant population estimates. As the dry season defecation rates had the strongest correlation with annual rainfall, the best period for assessing elephant density would be either the dry season or over the whole year. We do not recommend working during the wet season as this would add an additional variation in estimating elephant numbers due to large CV values.

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