

A COMPARISON OF REGRESSION-BASED ESTIMATES OF DUNG DECAY IN TWO AFRICAN FOREST DUIKER SPECIES (*PHILANTOMBA MONTICOLA*, *CEPHALOPHUS OGILBYI*)

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Abstract. Reliable dung decay rate estimates are essential for indirect surveys of forest ungulates, but there are still few reports of this parameter in the literature and there is a lack of consistency in their analytical assessment. In contrast to the standardized and statistically robust protocol for analyzing sign surveys of forest elephants, most duiker dung decay studies provide simple means only. We here report decay rates based on logistic regression on prospective data, collected at Korup National Park, Cameroon, based on 45 dung piles from Ogilby's duiker (*Cephalophus ogilbyi*) and on 23 dung piles from blue duiker (*Philantomba monticola*). Estimates were computed using maximum likelihood-based (R functions 'glm' as fixed and 'lmer' as mixed model specification), and quasi-likelihood-based ('lrm' and 'glmpql') logistic regressions. Ogilby's and blue duiker dung decay rates were estimated at 17 and 11 days on average, respectively. Decay rate estimates did not differ between mixed and standard models in blue duikers and only slightly in Ogilby's duiker. Our model-based decay rate estimates differed considerably from previously published dung decay rates and from arithmetic mean decay rates. Therefore we strongly suggest performing site- and time- specific dung decay experiments and utilizing logistic regression models to estimate dung decay to ensure robust duiker density estimations based on dung density.

Key words: dung survey, mixed-effects model, monitoring, rainforest, ungulate.

INTRODUCTION

Due to the poor visibility and elusive behavior of animals in dense and heavily hunted Afrotropical rainforests, indirect line survey techniques such as dung pile or nest surveys are often used for assessing wildlife abundance or densities (Muchaal & Ngandjui 1999, Plumptre 2000, Laing *et al.* 2003, Blom *et al.* 2005). Estimating animal density via dung surveys requires a reliable measure of decay and defecation rates of the observed dung. While defecation rates of duikers (Cephalophinae) seem to vary little, the few published dung decay rates vary by an order of magnitude (Koster & Hart 1988, White 1994, van Vliet *et al.* 2008, Breuer *et al.* 2009). Al-

though it remains unknown whether variation in dung decay is attributed to site-specific, seasonal, or method-related differences, some of these published dung decay rates (especially Koster & Hart 1988) are regularly used in duiker density estimations throughout Africa. This is clearly problematic, since decay rates seem to vary strongly with season, activity of insects such as dung beetles, or other factors (van Vliet *et al.* 2008, Breuer *et al.* 2009). Here, we report decay rate estimates for the two most common duiker species of Korup National Park (Ogilby's duiker *Cephalophus ogilbyi ogilbyi* and blue duiker *Philantomba monticola* (Waltert *et al.* 2006, Viquerat *et al.* 2012), and compare and discuss different decay estimation methods, ranging from educated guesses through observing a specific dung pile to average

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decay rates of individual piles, with the statistical estimates we produced.

MATERIAL AND METHODS

Study area and data acquisition. The study was conducted in the southern sector (5.044°N, 8.874°E to 5.071°N, 8.820°E) of the Korup National Park, Cameroon, near Chimpanzee Camp (5.069°N, 8.860°E). The vegetation of Korup National Park is classified as Biafran coastal forest, dominated by Caesalpinoid trees. The study area is less than 10 km away from the river Mana and the closest villages of “Ikondo Kondo 1, new settlement”, “Erat”, and the “Pamol plantation”. The area is intersected by many small to medium-sized creeks and rivers during the wet season and the few remaining medium-sized rivers in the west of the study area during the dry season (see also Astaras 2009). Our 3-month survey period ran from September to December 2009, which coincided with the end of wet season (late October 2009) and extended into the transition period between wet and dry season (November to early December 2009).

Twelve transects were made in a north-south direction, roughly 400 m apart from each other (“pseudo-random” placement) and each about 2 km in length. The total area covered by our sampling was approximately 13 km². Transects were repeatedly scanned for dung piles of Cephalophinae by a single observer in company of an experienced local hunter (for a mean number of 12 [minimum 9, maximum 13] times per transect) approximately every 3 days. The accompanying hunter came from a pool of 3 different hunters of approximately the same age.

A prospective approach to estimating dung decay rates (*sensu* Laing *et al.* 2003) was realized: any intact dung pile encountered on the transect for the first time was marked with a bright rubber band and its age roughly estimated by the assistant (relying solely on their extensive field experience and accounting for moisture and exposure to sun). As we also conducted a direct line transect survey at the same time on the same transects (Viquerat *et al.* 2012), transects (and the associated individual dung piles) were scheduled to be revisited every three days. Marked dung piles were re-located with the use of a GPS device and their status classified on each occasion as either intact or decayed. We thus gathered repeated data on individual dung piles, with each sample providing an initial (intact) age and a terminal (decayed) age. Due to the scheduling of fieldwork and possibly rapid

decay, not all samples could be monitored until decayed. Such dung piles were considered pseudo-replicates of intact dung piles.

Statistical analyses. We used two different logistic regression model approaches to estimate dung decay rates. Models based on maximum likelihood estimation of parameters were realized with the ‘glm’ function family of the statistical package R (as used in the CITES MIKE program; for details see Hedges & Lawson 2006 and R Development Core Team 2011), while models based on quasi-likelihood estimation were realized using the ‘lrm’ function from the Design package implemented in R (Harrell 2009). In order to assess study design effects due to transect placement, each category compares a standard (fixed effects only) model with a mixed-effect model (*sensu* Zuur *et al.* 2009) incorporating transect as a random error term.

We were mainly interested in explaining the response variable (“decayed” or “not decayed”) with time (measured in days). Individual dung piles only contributed the initial and the terminal age, thus avoiding possible pseudo-replication of intact dung piles that were sampled multiple times during the survey. However, dung piles that could not be observed until their status was “decayed” contributed to the pool of intact dung piles as pseudo-replicates. Outliers greater than 95% of the rest of the data were discarded due to the increasing inaccuracy of age estimation of dung older than 4 weeks. Since we suspected that the transect layout affected decay rate estimates due to (e.g.) variation in vegetation cover, steepness, or humidity, we also fitted mixed-effects logistic regression models specifying transect ID as random effect to account for these unmeasured factors. Models were compared based upon their parameter estimation. Since the application of mixed models requires the choice between maximum likelihood and quasi-likelihood approaches for parameter estimation, we chose to compare the most commonly used functions. For the quasi-likelihood approach, we chose the ‘lrm’ (Harrell 2009) function, while the maximum likelihood approach was realized by the ‘glm’ (R Development Core Team 2011) function as in the CITES MIKE program (Hedges & Lawson 2006, implemented in R by Mike Meredith). Both approaches were then compared with their respective mixed-effects equivalent ‘lmer’ (Bates *et al.* 2011) for maximum likelihood approaches, and ‘glmmPQL’ (from MASS package by Venables & Ripley 2002) for a penalized quasi-likelihood model

TABLE 1. Decay rates d (time to decay in days) of duiker dung from this study and other sources. Also given is the species and the model / method used to obtain decay rates. ML: maximum likelihood, QL: quasi-likelihood, mixed: inclusion of transect as error term, S.E.: standard error of the mean decay rate, % CV: % coefficient of variation of decay rate, NA: data not available.

<i>Species</i>	<i>Estimation approach</i>	<i>Method</i>	$d \pm SE$	% CV of d	<i>Source</i>
<i>C. ogilby</i>	'glm'	ML	16.97 \pm 1.49	8.77	This study
	'lmer'	ML (mixed)	17.08 \pm 1.69	9.87	
	'lrm'	QL	16.97 \pm 1.49	8.77	
	'glmmPQL'	QL (mixed)	17.11 \pm 1.62	9.44	
	Mean	-	8.44 \pm 1.01	79.94	
	Mean	-	1.35 \pm 0.93	68.89	Breuer <i>et al.</i> 2009
"red duikers"	Educated guess	-	4.30	NA	White 1994
	Mean	-	0.70 \pm 0.21	30	Van Vliet <i>et al.</i> 2008
	Mean (insects excluded)	-	17.30 \pm 1.42	8.10	
<i>C. monticola</i>	'glm'	ML	11.06 \pm 1.08	9.78	This study
	'lmer'	ML (mixed)	11.06 \pm 1.08	9.78	
	'lrm'	QL	11.06 \pm 1.08	9.78	
	'glmmPQL'	QL (mixed)	11.06 \pm 0.66	5.92	
	Mean	-	4.09 \pm 0.69	81.46	
	Educated guess	-	14	NA	Payne 1992
	Mean	-	1.13 \pm 1.04	92.04	Breuer <i>et al.</i> 2009

(Zuur *et al.* 2009). All models were fitted in R version 2.12.2 (R Development Core Team 2011; source code available from the first author). To emphasize the difference between the *mean decay rates of individual piles* approach prevalent in many duiker studies and *decay rate estimates from logistic regression* models, we discuss the two approaches based on the findings of the regression models and various literature sources.

RESULTS

A total of 45 dung piles of Ogilby's duiker and 23 dung piles of blue duiker were analyzed, most of which ($N = 37$ and $N = 15$ respectively) could be observed at multiple stages of decay (i.e., between intact and decayed). Both maximum likelihood and quasi-likelihood approaches produced average decay rate estimates of around 17 days (Ogilby's duiker) and 11 days (blue duiker) (Table 1). The standard model functions 'glm' and 'lrm' produced similar decay rates as their mixed-models counterparts 'lmer'

and 'glmmPQL'. Decay rate and associated standard error estimates from mixed models were slightly higher in Ogilby's (17.08 \pm 1.69 days in 'lmer', 17.11 \pm 1.62 days in 'glmmPQL', compared with 16.97 \pm 1.49 days in 'glm' and 16.97 \pm 1.49 days in 'lrm'; see Table 1).

Mean dung decay rate estimates for blue duikers did not differ between the fitted models, though the 'glmmPQL' model produced a considerably different standard error of decay rate (11.06 \pm 0.66 days compared with 11.06 \pm 1.08 days in 'lrm'; Table 1). However the penalized quasi-likelihood approach of 'glmmPQL' estimates variances differently and thus produces a different estimate of the standard error. These findings are also reflected in the results of the mixed-effects models. While there seemed to be a detectable variation in decay rates between transects in Ogilby duiker dung (standard deviation of random term: 0.53 in ML model, 0.65 in PQL model; see Table 2), blue duiker dung decay did not appear to vary between transects (Table 2).

TABLE 2. Random effects in Ogilby and blue duiker decay rates. Number of random effect groups indicates the number of random levels within the data (i.e. the number of transects available). ML: maximum likelihood, QL: quasi-likelihood, mixed: inclusion of transect as error term.

<i>Species</i>	<i>Model</i>	<i>Method</i>	<i>Standard deviation of intercepts</i>	<i>Number of random effect groups</i>
<i>C. ogilby</i>	'lmer'	ML (mixed)	0.53	9
	'glmmPQL'	QL (mixed)	0.65	9
<i>C. monticola</i>	'lmer'	ML (mixed)	0	10
	'glmmPQL'	QL (mixed)	≤ 0.01	10

DISCUSSION

Precision of dung decay rates. The % CVs (coefficient of variation of dung decay rate) from our logistic regression estimates ranged between 8.7 and 9.4 (5.9 for blue duiker decay estimated by 'glmmPQL'), which is far lower than most reported % CVs from decay rate studies in comparable settings (except for mean decay rates from red duikers "mean decay rate of individual piles under insect exclusion" by van Vliet *et al.* 2008, % CV = 8.1). However, given our 3-day interval of dung inspection, this high level of precision should be regarded cautiously. Dung decay due to beetle activity usually happens within a few hours (van Vliet *et al.* 2008) and these rapid decay processes may have therefore been missed by our survey design. Additionally, dung decay may not be constant over time but may be very dynamic, e.g. different stages of decomposition induce different decay rates, with fresh states decomposing fastest. Unfortunately, the limited sample size of dung piles did not allow more sophisticated statistical tests on this aspect. Uncertainty in prior knowledge of dung decay rates resulted in dung piles that could not be observed long enough for their status to change from intact to decayed. Adding these as pseudo-replicates to the pool of intact dung piles may have lead to bias in our estimates. However, we assume the bias due to the small sample size will outweigh the bias introduced by these pseudo-replicates.

All of the above points may lead to an overestimation of decay rates, since only decay processes longer than 3 days could be observed. However as the number of revisited individual piles was high, we assume the bias in decay rates produced by our survey to be small compared with previously published means of decay rates. Our own estimates from "mean decay rate of individual piles" were at roughly 50% of their logistic regression equivalents, which emphasizes the

importance of applying a logistic regression model and demands careful use of decay rate estimates from the literature.

As expected, "mean decay rate estimates" were associated with very high CVs (>75%), CVs similar to those provided by (e.g.) Breuer *et al.* (2009) (Table 1). This is important, since most temporal trend analyses are conducted via *z*-tests, and the coefficient of variation of an estimate is the key to identifying a change in the estimate (Plumpton 2000).

Comparing different analytical approaches. The generalized linear fixed-effects models 'glm' and 'lrm' produced similar results in the mixed models 'lmer' and 'glmmPQL'. It is noteworthy that considerable spatial variation in dung decay was discovered for Ogilby duikers but not for blue duikers (Table 2). These findings may suggest that dung decay conditions may differ at small spatial scales and may indicate that dung decay conditions could be species-specific.

Quasi-likelihood approaches such as 'lrm' and 'glmmPQL' in general suffer from the lack of available model comparison indices such as AIC or BIC (see Akaike 1974, Schwarz 1978). It would thus be difficult to fit more sophisticated models including covariates when sample sizes are small. Furthermore, the penalized quasi-likelihood approach in 'glmmPQL' makes its variance estimates difficult to compare with other studies not using a quasi-likelihood estimator when a change in decay rates is to be assessed.

Published duiker dung estimates often do not explicitly report which algorithm or model is used to produce the decay rate estimate, or they simply report arithmetic means of decay times. In contrast, the 'glm' logistic regression model is widely applied in elephant dung surveys (Hedges & Lawson 2006, or e.g. CITES approach, MIKE program) and the ap-

parent under-utilization of this approach in duiker dung surveys is very surprising, given its relative ease of use in standard statistical software (Zuur *et al.* 2009, CITES R script available at http://www.wcs-malaysia.org/analysis/ZIP/Nakai_dung_disapp.zip, last accessed 16.07.2013). Comparing different modelling approaches suggests that estimated mean decay rates are broadly insensitive to the specific model formulation. We thus advise the use of generalized linear models based on maximum likelihood estimation in any decay rate study, whether as generalized linear model or, if the study design allows, as a generalized linear mixed model approach (Laing *et al.* 2003); see also chapter 13 in Zuur *et al.* (2009).

Dung decay in context. We found our binomial regression decay rates being very similar to those from an earlier study (Payne 1992) done in the same region (Korup National Park) and habitat type (primary forest), as well as to those from van Vliet *et al.* (2008) for dung piles where insect attack was experimentally excluded. However, a comparison with simple means only is questionable since effects due to study design cannot be detected by arithmetic means. A difference in our estimates of up to an order of magnitude compared with an estimate based upon dung piles that had not been manipulated (van Vliet *et al.* 2008), as well as with those of White (1994) and Breuer *et al.* (2009), cannot be easily explained retrospectively.

The questions why and how decay rates vary is far from being exhaustively answered. In 'red duikers' (*C. callipygus* and *C. dorsalis*), the decay rate was found to be affected strongly by insect attack, dung beetles potentially being the most effective guild, with the effect decreasing towards the end of the rainy season (van Vliet *et al.* 2008). White (1994) even observed an increase in decay times of about 1500%, from 4.3 days during the wet season to more than 2 months during the dry season. However, in White's (1994) study site hunting was effectively banned, and we thus assume a high abundance of large mammals and hence a comparatively higher dung beetle abundance compared with Korup National Park. This may explain his high decay rate (short decay time) during the wet season.

For a better understanding of the ecological factors affecting decay rates, further field research is required. Since a number of factors may influence decay rate, the flexibility of models clearly surpasses the performance of arithmetic means to identify these. In order to obtain robust estimates, we recom-

mend – in contrast to our own approach – daily sampling of dung piles, which improves temporal resolution of dung decay and would allow rapidly decaying dung piles to be observed. Additionally, to ascertain comparability with other studies dung surveys should be conducted independently of other survey activity.

ACKNOWLEDGMENTS

We thank Christoph Scherber, Christos Astaras, the Arong family, Celestine & Jonas Awoh, Innocence Motia, Roland Modika, Mambo Peters, Chief Philip, Orume Robinson, Chief Simon and all of the Eco-guards. We also thank the Ministry of Forests and Wildlife (MINFOF) and the Ministry of Scientific Research and Innovation (MINRESI) for permission to carry out research in Korup National Park. This study was financially supported through a grant from the Volkswagen Foundation, Hannover, Germany, to the universities Dschang and Göttingen within its project "Africa Initiative - Knowledge for Tomorrow: Cooperative Research Projects in Sub-Saharan Africa".

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