The survival of elephant dung piles in relation to forest canopy and slope in southern Ghana

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Abstract

Dung piles were monitored from deposition to disappearance in three Ghanaian forests. Cox proportional hazard models were fitted to the data to explain the variables that had the greatest influence on dung survival under open canopy and closed forest (< 75% and ≥ 75% canopy cover respectively) after adjusting for rainfall. For dung piles in closed forest, canopy cover and slope were important predictors of hazard, and one site was markedly different from the other two. The open canopy subsample did not conform to the assumption of the proportional hazards method. Dung decay observations must always be conducted in sites where a dung count survey is done to estimate elephant numbers. The observed dung piles must reflect the occurrence of all vegetation types to avoid bias in the final estimate of elephant abundance.

Résumé

On a surveillé régulièrement des tas de crottes, à partir du moment où ils étaient constitués jusqu’à leur disparition, dans trois forêts ghanéennes. Les modèles à risques proportionnels de Cox ont été adaptés aux données pour expliquer les variables qui avaient la plus grande influence sur la conservation des crottes sous une canopée ouverte ou une forêt très fermée (< 75% et ≥ 75% de couverture respectivement) après avoir ajusté les données aux chutes de pluie. Pour les tas de crottes situés en forêt fermée, la couverture et la pente étaient d’importants indicateurs de risques, et un site était nettement différent des deux autres. Le sous échantillon situé sous la canopée ouverte ne se conformait pas aux suppositions de la méthode des risques proportionnels. Il faut toujours faire des observations de décomposition des crottes dans des endroits où une étude du comptage des crottes sert à évaluer le nombre d’éléphants. Les tas de crottes observés doivent refléter la présence de tous les types de végétation pour éviter tout biais dans l’estimation finale de l’abondance des éléphants.

Introduction

Dung counts can provide estimates of elephant numbers that are just as accurate as other survey methods, and their estimates are more precise (Barnes 2001, 2002). However, they must be conducted scrupulously if they are to provide accurate and precise estimates. The three variables that must be estimated are dung pile density, defaecation rate and dung-disappearance rate. This paper addresses the third variable.

The survival time is inversely proportional to the rate of dung disappearance. It is the time between deposition and the point when the dung pile is judged to have disappeared (stage E of Barnes and Jensen 1987, or stage S4 as defined in Hedges and Lawson 2006). In any given site dung piles show a remarkable variation in their survival times; some disappear rapidly while close neighbours last for weeks. A representative sample of dung piles must be monitored to obtain an unbiased estimate of the decay rate. However, finding a sample of dung piles is often difficult when elephants are sparse. Sometimes large numbers of fresh dung piles are found in one spot, and tired and frustrated field assistants will be tempted to mark them all. It may be difficult to convince the field teams of the need to search more widely for a representative sample. If we understand the variables that determine the survival time, then field assistants will invest more effort in searching for dung piles.

Rainfall is clearly the most important factor governing dung-decay rates (White 1995; Barnes et al. 1997; Nchanji and Plumptre 2001). Canopy cover and slope vary across every study area, and here we examine their effect on dung survival after adjusting for rainfall. The data come from 1993 and 1994 when we estimated survival times in both wet and dry seasons in three forests in southern Ghana (Barnes et al. 1994, 1997). We fit statistical models that are uncommon in ecology but frequently used in other fields.

Methods

Study sites

This study was conducted in three protected forests in southern Ghana: Ankasa Game Production Reserve, Bia Game Production Reserve and Kakum National Park/Assin Attandanso Game Production Reserve. They were described briefly in Barnes et al. (1997) and in more detail by Barnes et al. (1994).

Field methods

Methods were standardized across sites. At each site a sample of fresh dung piles (< 48 hours since deposition) was marked in the wet and dry seasons and observed at weekly intervals. When the dung pile passed from morphological stage D to stage E (Barnes and Jensen 1987), it was recorded as 'disappeared'.

The angle of slope was measured with a clinometer. A photograph looking vertically upwards was taken by lying down next to the dung pile. Later the area of the photograph covered by foliage was measured with a dot grid to give the percentage of canopy cover over the dung pile.

Rain gauges were established at each site. Three rainfall variables were collected: $RAIN_{10}$ was the rainfall that fell during the first 10 days after deposition of each dung pile, $RAIN_t$ was the rainfall during the calendar month of deposition while $RAIN_{t+1}$ was the rainfall in the calendar month after the month of deposition. Preliminary analysis showed that only $RAIN_t$ had a strong relationship with dung survival, and the other two were discarded.

Analysis

A total of 427 dung piles were marked and observed in the three forests for 18,217 dung-pile days. Covariates had not been measured for some dung piles, and their elimination reduced the number to 358. Three of these were either lost or had not decayed by the time observations ceased; they were treated in the analysis as *censored* cases (Collett 1994).

The sample spanned a wide range of canopy values, from 0 to 99%. The dung piles with lower canopy values were in clearings, on roads or at the forest edge. They will be more susceptible to wind, sunshine and higher temperatures, and the humidity regime will differ from closed forest. Therefore, the sample was split into two, an outside subsample with canopy values < 75% and a closed forest subsample with canopy values of 75% or more.

The survivor function is the probability that a dung pile survives from the time of deposition to a time beyond *t*. The hazard function is the probability that a dung pile disappears (i.e. passes to stage E or S4) at time *t*, conditional upon it having survived to that time. Or put another way, the hazard function represents the instantaneous disappearance rate for a dung pile surviving to time *t* (Collett 1994).

By fitting a model one can examine the effect of several potential explanatory variables upon the survival of a sample of dung piles. Once one has added a rainfall variable to the model one can then examine the effect of individual variables, such as canopy cover or slope, on the survival function. One may also determine the best combination of variables that influence the hazard function. We fitted a proportional hazards model (Cox 1972; Collett 1994):

$$h_i(t) = \exp(\beta_1 x_{1i} + \beta_2 x_{2i}) h_0(t)$$

which can be re-expressed as:

$$\log \{h_i(t) / h_0(t)\} = \beta_1 x_{1i} + \beta_2 x_{2i}$$

where $h_i(t)$ is the hazard function for the *i*th dung pile at time *t*, and $h_0(t)$ is the hazard function for a dung pile for which the values of all the variables are zero, for example when there is no rain and the dung pile lies on a flat area. x_1 and x_2 are covariates, such as rainfall and slope, while b_1 and b_2 are regression coefficients. This is therefore a linear model for the log of the hazard ratio. Here only two covariates have been shown, but more can be added.

The proportional hazards model was fitted by maximum likelihood. The change in –2log*L* when fitting a new variable was compared with χ^2 for one degree of freedom to evaluate the importance of that variable (Collett 1994).

First we fitted each independent variable by itself. The results indicated the importance of each variable alone. Then we started the model-building process. Since we know from previous work that rainfall is the most important predictor of dung decay (White 1995; Barnes et al. 1997; Nchanji and Plumptre 2001), rainfall was added to the null model. Then the other covariates were added one at a time. We retained the one that produced the greatest reduction in –2log*L* (i.e. the one with the highest value of χ^2) when added to the model. The remaining covariates were added one at a time, and again the one causing the greatest reduction in –2log*L* was retained. This continued until no further significant reduction of –2log*L* resulted.

We applied the test described by Hosmer and Lemeshow (1999) to check that the assumptions of the proportional hazards model were satisfied. After the main-effects model had been derived, another model was fitted using the main-effects model and the interaction of each covariate with log(time) or *ln(t).* Hosmer and Lemeshow (1999) advise centring log(time) about its mean [$ln(t) - \overline{ln(t)}$] for numerical reasons.

If the hazard function appears to be proportional, one can then proceed to refine the model by examining interactions (Collett 1994). The Akaike Information Criterion (AIC) was used to compare models: the smaller the value of AIC the better the model (Collett 1994).

To adjust for possible differences between sites, indicator variables (Collett 1994) SITE1 and SITE2 were defined (table 1).

Table 1. Indicator variables to distinguish between sites

Study area	SITE1	SITE2
Ankasa	0	0
Bia	1	0
Kakum	0	1

Results

Closed canopy

There were 291 dung piles in the closed forest subsample where canopy cover is ≥75%. For these dung piles, three variables when added by themselves to the null model produced a significant reduction in –2log*L* (table 2). $RAIN_t$ was confirmed to be the best predictor of hazard.

The *SITE2* covariate was also significant, showing that Kakum had a lower hazard than Ankasa and Bia. The third covariate was *CANOPY:* the greater the canopy cover, the slower the rate of dung decay.

Next, having adjusted for $RAIN_t$, the best predictive model was obtained by examining the effect of each of the other covariates. This model included *SLOPE* and *SITE2* as well as $RAIN_t$ (table 3). This means that after adjusting for rainfall, the angle of slope was a very important predictor of hazard. The risk of disappearance increased by about 8% for each 1º increase in slope. Even after taking rainfall and *SLOPE* into consideration, there remained a significant difference between Kakum and the other two sites.

This model was tested for proportional hazards by adding the interaction terms with log time (table 4). There is no evidence to doubt the assumption of proportional hazards because each of the interaction terms was insignificant (Hosmer and Lemeshow 1999).

Interaction terms *for* $RAIN_t$**SLOPE*, $RAIN_t$**SITE2* and *SLOPE*SITE2* were added to the model. Two out of the three were retained (table 5). Adding these interaction terms reduced the AIC from 2646.58 to 2631.65, and the reduction in –2log*L* was significant ($\chi^2 = 18.93$, $P < 0.001$). Note that the coefficient for *SLOPE* was not significant, but it was retained in this model to conform to the hierarchic principle (Collett 1994).

Open canopy

There were 67 dung piles where canopy cover is < 75%. First, a model was fitted to each independent variable alone. As expected, rainfall was a significant predictor of hazard (table 6). However, *CANOPY* was the strongest predictor. Note that increasing canopy was associated with a higher hazard.

Table 2. Closed forest: proportional hazard estimates for each independent variable fitted by itself to the null model

Variable in model	β	s.e. (β)	χ^2	Hazard ratio	95% confidence limits for hazard ratio
SITE1	0.221	0.125	3.12	1.247	0.976–1.592
SITE2	–0.299	0.119	6.29*	0.742	0.587–0.937
CANOPY	–0.019	0.009	4.05*	0.982	0.964–1.000
SLOPE	0.009	0.014	0.36	1.009	0.981–1.038
$RAIN_t$	0.006	0.001	57.14****	1.006	1.005–1.008

* $P < 0.05$; ****$P < 0.0001$

Table 3. Closed forest: the best combination of variables in the proportional hazards model (AIC = 2646.58)

Variable in model	β	s.e. (β)	χ^2	Hazard ratio	95% confidence limits for hazard ratio
$RAIN_t$	0.007	0.001	61.76****	1.007	1.006–1.009
SLOPE	0.078	0.017	20.49****	1.082	1.045–1.119
SITE2	–0.451	0.144	9.80**	0.637	0.480–0.845

**$P < 0.01$; ****$P < 0.0001$

Table 4. Closed forest: test for proportionality (AIC = 2650.04)

Variable in model	β	s.e. (β)	χ^2	Hazard ratio	95% confidence limits for hazard ratio
$RAIN_t$	0.007	0.001	62.77****	1.007	1.006–1.009
SLOPE	0.081	0.018	21.27****	1.084	1.048–1.122
SITE2	–0.464	0.145	10.22**	0.629	0.473–0.836
$RAIN_t$*ln(t)	–0.001	0.001	0.28	0.999	0.997–1.002
SLOPE*ln(t)	–0.042	0.034	1.58	0.959	0.898–1.024
SITE2*ln(t)	0.160	0.287	0.31	1.173	0.668–2.059

**$P < 0.01$; ****$P < 0.0001$

Table 5. Closed forest: the final proportional hazards model that includes main effects and interaction effects (AIC = 2631.65)

Variable in model	β	s.e. (β)	χ^2	Hazard ratio	95% confidence limits for hazard ratio
$RAIN_t$	0.005	0.001	28.07****	1.005	1.003–1.007
SLOPE	–0.044	0.037	1.45	0.956	0.890–1.028
SITE2	–0.980	0.214	20.97****	0.375	0.247–0.571
$RAIN_t$*SLOPE	0.001	0.000	13.54***	1.001	1.000–1.002
SLOPE*SITE2	0.105	0.037	7.95**	1.111	1.033–1.195

**$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$

Table 6. Dung piles under open canopy (canopy cover < 75%): proportional hazard estimates for models fitted to each independent variable alone

Variable in model	β	s.e. (β)	χ^2	Hazard ratio	95% confidence limits for hazard ratio
SITE1	–0.119	0.261	0.21	0.887	0.532–1.481
SITE2	–0.063	0.252	0.06	0.939	0.573–1.540
CANOPY	0.014	0.006	6.26*	1.014	1.003–1.026
SLOPE	0.023	0.030	0.60	1.023	0.965–1.084
$RAIN_t$	0.003	0.002	3.88*	1.003	1.000–1.006

* $P < 0.05$

In the next step, we obtained the best predictive model for open canopy by first fitting $RAIN_t$ and then adding each of the other variables in turn. The model that produced the greatest reduction in –2log*L* (χ^2 = 9.52, df = 2, $P < 0.01$) included only $RAIN_t$ and *CANOPY* (table 7). But note that in this model the coefficient for $RAIN_t$ was not significant.

Both interaction terms with *ln(t)* were large and significant (table 8). When $RAIN_t$ alone was tested with $RAIN_t$**ln(t)*, the interaction term was significant at $P < 0.0001$, and the same was true for *CANOPY* and *CANOPY*ln(t)*. These tests show that the proportional hazard assumption is violated for this subsample.

Discussion

Methodology

The proportional hazards method assumes that the difference in hazard due to a particular covariate remains constant. For example, Kakum's hazard is 26% less than hazard in the other two sites (table 2), and that difference should hold throughout the process of decay. If it changes as a dung pile gets older, then the method of proportional hazards is no longer valid. We cannot explain why the assumption appears to hold for the closed forest subsample but not for the open subsample. It may be a consequence of an inadequate sample size for the open canopy—only 67 dung piles compared with 291. Where proportional hazards are inappropriate, the non-parametric Kaplan-Meier method may be used to estimate the hazard function (M. Sivaran, pers. comm.). The advantage of the Cox proportional hazards method is that it allows one to evaluate the influence of several covariates.

In the present study dung piles were monitored from the time of deposition until they disappeared. Thus the exact survival time of each dung pile was known and a survival model could be fitted. However the data-collection phase was very time consuming as each dung pile had to be visited at regular intervals. In the future, dung-disappearance rates and the effect of covariates will be estimated more efficiently by Laing et al.'s (2003) method that requires that each dung pile be seen only twice.

Closed forest

Under a dense forest canopy the probability of disappearance (i.e. passing from stage D to E or from stage S3 to S4) for a dung pile depended upon three variables. Rainfall was confirmed to have the greatest influence upon survival or dung-decay rate, as others have shown (White 1995; Barnes et al. 1997; Nchanji and Plumptre 2001). An increase of 1 mm of rainfall would increase the hazard by 1.006 (table 2). For example, if month B had 100 mm more rainfall than month A, the hazard would be 1.006^{100} = 1.82 times greater in month B.

Slope and rainfall together were significant ($P < 0.001$) but the effect was small (hazard ratio = 1.001;

Table 7. Dung piles under open canopy (canopy cover < 75%): estimates for the variables included in the best proportional hazards model (AIC = 432.64)

Variable in model	β	s.e. (β)	χ^2	Hazard ratio	95% confidence limits for hazard ratio
$RAIN_t$	0.002	0.002	2.37	1.002	0.999–1.005
CANOPY	0.013	0.006	5.04*	1.013	1.002–1.025

* $P < 0.05$

Table 8. Dung piles under open canopy (canopy cover < 75%): test for the assumption of proportional hazards (AIC = 289.44)

Variable in model	β	s.e. (β)	χ^2	Hazard ratio	95% confidence limits for hazard ratio
$RAIN_t$	0.003	0.002	1.54	1.003	0.998–1.007
CANOPY	0.047	0.010	21.49*	1.048	1.028–1.069
$RAIN_t$*ln(*t*)	–0.016	0.005	9.31**	0.984	0.974–0.994
CANOPY*ln(*t*)	–0.133	0.022	37.16****	0.876	0.839–0.914

*$P < 0.05$; **$P < 0.01$; ****$P < 0.0001$

table 5). On the other hand, this was in addition to the effect of rainfall (hazard ratio = 1.005; table 5). The effect of slope was particularly marked at Kakum, as revealed by the *SLOPE*SITE2* interaction.

After allowing for rainfall and slope, there was a major difference in hazard between Kakum on the one hand and Bia and Ankasa on the other (table 5). This could be due to differences between the field teams, for example in judging when a dung pile had 'disappeared'. However, the teams were trained carefully to avoid this sort of problem. The difference is probably due to covariates that were not included in the model, such as soil type or the presence of animals or birds that rummage through dung piles in search of seeds. This emphasizes the point that dung-decay observations must be conducted at every site where a dung count is conducted.

When considered by itself, canopy cover reduced the hazard (table 2): dung piles lasted longer under the densest canopy. However this effect did not appear in the final model after accounting for $RAIN_t$, *SLOPE* and *SITE2* (tables 3 and 5).

Open forest

Interpretation of the results from open forest must be limited because the proportional hazard assumption did not hold. We make just two comments. First, the hazard appeared to increase with canopy cover (table 7). In other words, dung piles lasted longer in more open areas, probably because they dried out soon after deposition (White 1995). This is in contrast to closed forest (table 2), where dung piles lasted longer under completely closed canopy but is consistent with the observations of Nchanji and Plumptre (2001), who had a range of canopy from 51% to 77%. Second, in contrast to closed forest, after adjusting for rainfall there was no evidence that slope was important in these open places.

Conclusion

The marked difference between sites—especially after adjusting for slope, canopy and rainfall—illustrate the necessity for estimating dung-decay rates at the site where an elephant dung census is to be conducted. One can no longer justify using dung-decay estimates from similar sites.

Canopy was a significant predictor in the absence of the other covariates in this closed forest subsample. It may also be important in more open habitats. Slope was also an important predictor. This means that when planning a dung-count survey, the monitored dung piles must be distributed so as to cover the range of canopy and slope values that will be included in the line transects. One cannot choose a convenient sample of dung piles in a flat area near camp, for that will give a biased estimate of the rate of disappearance. Therefore, as much importance must be given to the selection of dung piles for estimating decay rates as to the placement of line transects. In other words, habitat types must be represented in proportion to their occurrence, for example, by searching for dung piles along randomly or systematically placed transects (Buckland et al. 2001; Laing et al. 2003).

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