Rapid dung removal by beetles suggests higher duiker densities in Central African rainforests

AUTHOR(S):

Kamgaing, Towa Olivier William; Dzefack, Zeun's Célestin Brice; Dongmo, Nago Charleine Blondèle; Tchatat, Maturin; Yasuoka, Hirokazu

CITATION:

Kamgaing, Towa Olivier William ...[et al]. Rapid dung removal by beetles suggests higher duiker densities in Central African rainforests. Oryx 2023, 57(2): 180-187

ISSUE DATE:

2023-03

URL:

http://hdl.handle.net/2433/281915

Rapid dung removal by beetles suggests higher duiker densities in Central African rainforests

Towa Olivier William Kamgaing, Zeun's Célestin Brice Dzefack
Nago Charleine Blondèle Dongmo, Maturin Tchatat and Hirokazu Yasuoka

Abstract For many mammal species, converting dung density into population density requires accurate estimates of defaecation rate and dung survival time. The latter parameter probably varies seasonally. In Nki National Park, south-east Cameroon, we monitored 216 dung piles of the blue duiker *Philantomba monticola* and 373 of the red duiker group (*Cephalophus* spp.), major game animals in Central Africa, and estimated dung survival time across seasons. Mean survival time was 6.83 days in the major dry season and 1.21–1.81 in other seasons for the blue duiker, and 7.37 and 1.53–4.05 for red duikers, lower than the values conventionally used for density estimations in Central Africa (i.e. 18 days for the blue duiker and 21 days for red duikers). Overall, beetles removed half of the dung within 1 day of deposition. However, the proportion of dung piles that beetles removed was significantly lower in the major dry season, and other dung piles remained longer until they disappeared as a result of other factors. As shorter dung survival time results in higher estimates of population density, our findings imply that in forests with intense beetle activity, duiker densities are higher than those based on the conventional values of dung survival time. Duiker densities and dung survival time should be estimated simultaneously. To minimize the bias introduced by rapid removal of fresh dung by beetles, only fresh dung (< 3 hours old) should be monitored when estimating mean dung survival time.

Keywords Bushmeat hunting, Cameroon, density estimation, duiker, dung decay, dung survival time, Nki National Park, wildlife management

Towa Olivier William Kamgaing (Corresponding author, orcid.org/0000-0002-5653-9019, kamgaing@jambo.africa.kyoto-u.ac.jp) and Hirokazu Yasuoka (orcid.org/0000-0001-5066-1534) Center for African Area Studies, Kyoto University, 46 Yoshida-Shimoadachi, Sakyo, Kyoto, 606-8501, Japan

Zeun's Célestin Brice Dzefack University of Dschang, Dschang, Cameroon

Nago Charleine Blondèle Dongmo Centre Régional d'Enseignement Spécialisé en Agriculture Forêt-Bois, Yaoundé, Cameroon

Maturin Tchatat Institute for Agricutural Research and Development, Yaoundé, Cameroon

Received 23 February 2021. Revision requested 2 July 2021.
Accepted 29 October 2021. First published online 18 March 2022.

Introduction

The expansion of the logging road network in West and Central Africa has facilitated access to forest for poachers and bushmeat traders (Robinson et al., 1999). Forest dwellers engage in the bushmeat trade to a greater or lesser extent (Yasuoka, 2006; Martin et al., 2020), and the depletion of wildlife populations and declining food supplies threaten people's livelihoods and have resulted in the bushmeat trade becoming a global concern (Wilkie & Carpenter, 1999; Fa et al., 2002; van Vliet & Nasi, 2008; Ichikawa, 2014; Yasuoka et al., 2015).

Against this background, conflicts have arisen between local people and conservationists (Pyhälä et al., 2016). One of the reasons for these conflicts is the lack of reliable, and the sometimes controversial, information on the abundance of wild animals, including duikers, the major game animals in Central Africa (van Vliet & Nasi, 2008; Elenga et al., 2020). Estimated population densities of game species may differ by 10-fold or more depending on the survey methods used (Koster & Hart, 1988; Wilkie & Finn, 1990; Jost Robinson et al., 2017; Kamgaing et al., 2018). Management decisions based on unrealistic estimates could lead to unnecessary conflicts, and it is therefore essential that conservation agencies share accurate information with local people.

In dense tropical forests, wildlife surveys are usually challenging because of poor visibility and the shyness of wild animals (Elenga et al., 2020). Therefore, rather than attempting to quantify numbers directly, indirect survey techniques such as counts of animal signs (e.g. dung piles of ungulates or nests of primates) are used (White & Edwards, 2000). Dung survey is the most frequently used method to estimate the population density of forest duikers. Of 65 published duiker densities in Central Africa, 33 were based on dung surveys (Supplementary Table 1), including in the Democratic Republic of the Congo (Koster & Hart, 1988; Wilkie & Finn, 1990), Cameroon (Payne, 1992; Ekobo, 1998; Yasuoka, 2006; Bobo et al., 2014; Nzooh-Dongmo et al., 2016; Kamgaing et al., 2018), Gabon (Koerner et al., 2017) and the Republic of the Congo (Breuer et al., 2021).

To estimate animal density based on dung survey, accurate values of dung density, defaecation rate and mean dung decay time are required. The number of animals in a given area is the number of observed dung piles divided by the number of dung piles that an individual defaecates per day (defaecation rate) and by mean dung decay time (White & Edwards, 2000; Marques et al., 2001; Thomas et al., 2010). To our knowledge, these parameters were estimated for the blue duiker *Philantomba monticola* and red duikers *Cephalophus* spp. for the first time in the Democratic Republic of the Congo (Koster & Hart, 1988), and are still used in most publications on duiker density. Of the 33 density estimates we are aware of, 27 used the values of dung decay time from Koster & Hart (1988): 18 days for the blue duiker and 21 days for red duikers. These values are the maximum dung decay times estimated in a single, dry season from captive duikers.

Two key problems hinder the accurate estimation of duiker density from dung. Firstly, there is a lack of data on dung decay time and the effect of season on this. The use of dung decay time calculated in other localities or seasons to estimate duiker density in a given area is likely to result in biased duiker densities, as dung decay may be influenced by factors such as climate, diet and insect activity (Koster & Hart, 1988; van Vliet et al., 2009). Because most dung piles disappear not as a result of decay but as a result of other factors, we use the term dung survival time rather than dung decay time.

Secondly, the effect of the freshness of dung on the measurement of dung survival time needs to be considered. The few published values of dung survival time for duikers were calculated from dung piles 0–24 hours old (Beukou et al., 2019) or pellets collected from duiker intestines (van Vliet et al., 2009). Other studies have simply reported that fresh or intact dung was used (Breuer et al., 2009, 2021; Viquerat et al., 2013).

We address these problems by monitoring the dung of duikers and analysing factors influencing dung survival time in Nki National Park, south-east Cameroon. We also compare dung survival time for the blue duiker and red duikers across seasons.

Study area and species

This study was conducted in Nki National Park, south-east Cameroon, Central Africa (Fig. 1). The climate of the region is characterized as a four-season equatorial climate, with a major dry season during December–February, a minor wet season during March–June, a minor dry season during July–August and a major wet season during September–November (Ekobo, 1998). Mean annual rainfall is c. 1,660 mm and mean annual daily temperature is 23 °C (Supplementary Fig. 1). The main vegetation type is a mixture of evergreen and semi-deciduous forests (Letouzey, 1985).

Two main groups of people live in this area: the Baka and the Bantu. Both groups cultivate subsistence crops such as plantain and cassava. Cocoa farming is the main source of income for the Bantu. Bushmeat hunting and gathering of non-timber forest products are also widely practised. The main hunted species are duikers, the porcupine *Atherurs africanus* and monkeys *Cercopithecus* spp. (Yasuoka, 2006, Bobo et al., 2015, Martin et al., 2020).

There are six species of duiker recorded in the forests of south-east Cameroon: the small blue duiker *Philantomba monticola* (3.5–9.0 kg), the large yellow-backed duiker *Cephalophus silvicultor* (45.0–80.0 kg), and four medium-sized species with reddish fur (Peters's duiker *Cephalophus callipygus*, 17.5–25.2 kg; bay duiker *Cephalophus dorsalis*, 15.0–24.5 kg; white-bellied duiker *Cephalophus leucogaster*, 15.0–20.0 kg; black-fronted duiker *Cephalophus nigrifrons*, 14.0–18.0 kg). As the dung of medium-sized duiker species is difficult to distinguish, we grouped these four species into a single category, red duikers.

Methods

Data collection

We established four 2-km transects, 400–800 m apart, in Nki National Park (Fig. 1). To maximize the number of dung piles, we opened two parallel paths, 4 m either side of each transect, giving a total of 12 observation paths. We surveyed the transects in January–May 2019, August–December 2019, January–February 2020 and May 2020. Together with three experienced local hunters, we searched for dung piles of duikers between 07.00 and 17.00. Each observer walked along a path but could move several metres away from the path if required. Only dung piles considered to be no older than 1 day (see below) were recorded. Dung of the yellow-backed duiker was rare and therefore not included in the analysis.

When a dung pile was detected, we assigned a unique identifier, measured the diameter covered by pellets, and estimated how many hours ago it had been deposited. Although it was not possible to know the exact time of the defaecation, experienced trackers and researchers can reasonably estimate their age (Viquerat et al., 2013; Elenga et al., 2020). We inspected the appearance of dung piles (shine, moisture) and other factors such as associated presence of urine, time of last rain and exposure to sun. In discussion with the experienced hunters, we agreed upon when the dung was deposited, classifying dung piles into age classes of 3 hours (hereafter referred to as age class at detection).

Dung piles were then visited twice per day to check whether they had disappeared or still remained, and in the case of the former, to determine what had caused their disappearance: removal by beetles, decomposition, washed away by rain, covered by fallen leaves, or other. As we monitored the dung daily, we were able to identify the factor responsible for disappearance with confidence. We sometimes

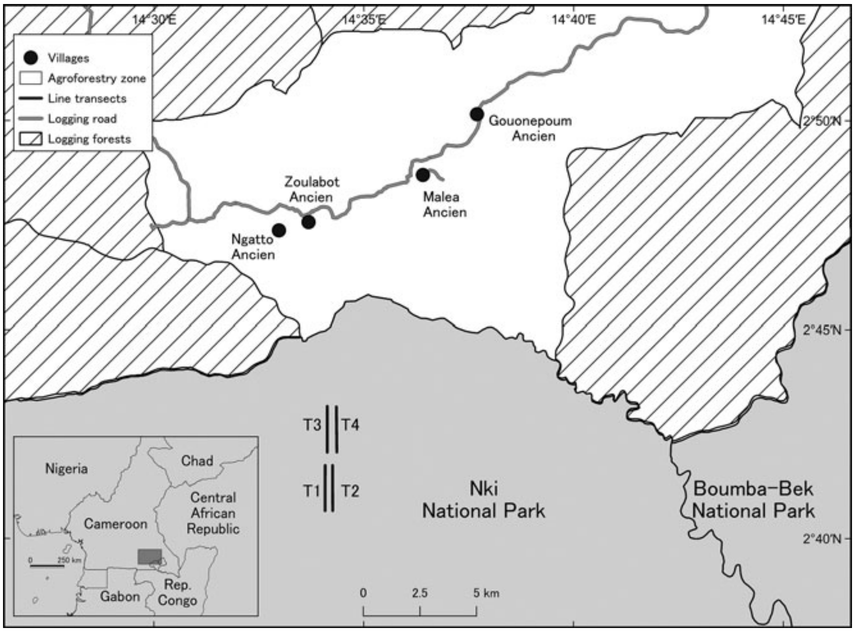

FIG. 1 The study area in Nki National Park, south-east Cameroon, with the location of villages, and transects (T1–4) established for monitoring the disappearance of the dung of blue duiker *Philantomba monticola* and red duikers *Cephalophus* spp.

observed dung beetles removing fresh pellets completely within a few hours of detection and therefore when fresh dung disappeared within a day, we considered beetles had removed them. In contrast, decomposition was gradual. Rainfall can wash away dung, but we could distinguish this from removal by beetles. When a dung pile disappeared rapidly, we checked whether it had been covered by fallen leaves, recording 'leaf cover' if this was the case. Cover by fallen leaves will affect density estimation in the same way as removal by beetles, as such dung is unlikely to be recorded during a dung survey.

Inspecting dung piles twice daily allowed us to record survival time with precision. To facilitate this monitoring, we camped near the paths for c. 8 days at a time, with 3–4 day breaks between surveys. In total, individual dung piles were visited 2–34 times, in contrast to retrospective surveys, in which animal signs are marked and revisited once to record whether they have disappeared or not (Laing et al., 2003). A dung pile was categorized as disappeared when it was no longer recognizable as a dung pellet group (Marques et al., 2001; van Vliet et al., 2009). We determined the main factor causing each dung pile to disappear by examining the dung remnants or the spot where each dung pile was dropped and, when necessary, by comparing these observations with photographs of the pellets taken at each visit.

Data analysis

As there were 3- to 4-day intervals between each 8-day survey, we occasionally missed the exact date when some dung piles disappeared, but knew the two dates between which they disappeared. In these cases, we used the mid point of the two dates for calculating the survival time. The impact of these mid-point data on the variance of survival time estimates is probably negligible because such data comprised only 7% of the observations and because of the short intervals between observations (Bogaerts et al., 2018, chapter 4).

To visualize the relationship between the estimate of dung survival time and age class at detection, we categorized dung piles into four overlapping age classes at detection: 0–3 hours, 0–6, 0–12 and 0–24. To evaluate any effect of age at detection, we fitted a generalized linear model (GLM) to dung survival time with absolute age at detection as the single explanatory variable. Mid-point data were excluded from this analysis. Because age at detection had a significant effect on survival time estimates, we discarded dung piles detected at an older age (i.e. dung piles that were not fresh upon detection) before further analysis. In addition, we discarded the top 0–4% of outliers that did not decay for longer periods (in total, five dung piles of the blue duiker and eight of red duikers), to avoid a substantial decrease in the precision of mean survival time estimates but maintain accuracy (Viquerat et al., 2013).

We then calculated mean dung survival time for each season using two approaches: a GLM including only season as the explanatory variable, and simple arithmetic means. Mid-point data were excluded from calculation of arithmetic means but included for the analysis using a GLM.

To evaluate the effect of season, the main factor causing dung disappearance and dung pile diameter (the latter $\log_{10}$ transformed) on dung survival time, we fitted GLMs with a gamma error distribution and log-link function as the response variable (survival time) was non-negative. Spatial autocorrelation of factors causing disappearance, in particular of beetle attack, on neighbouring dung was probably

TABLE 1 Mean ± SE dung survival time of the blue duiker *Philantomba monticola* and red duikers *Cephalophus* spp. in Nki National Park, south-east Cameroon (Fig. 1), by season, calculated with a generalized linear model (GLM) and as arithmetic means.

		Survival time (days)			
Taxon/season	Method	Mean ± SE	Range	Median	Sample size
Philantomba monticola					
Major dry	GLM	6.83 ± 1.17	0.13–34.20	3.15	50
	Arithmetic mean	5.81 ± 0.25	0.13–34.20	1.00	40
Minor wet	GLM	1.20 ± 0.17	0.13–11.20	1.00	72
	Arithmetic mean	1.08 ± 0.02	0.13–6.00	0.25	71
Minor dry	GLM	1.81 ± 0.38	0.25–17.20	1.00	33
	Arithmetic mean	1.99 ± 0.07	0.25–14.20	1.00	33
Major wet	GLM	1.72 ± 0.27	0.13–9.25	1.30	61
	Arithmetic mean	1.73 ± 0.03	0.13–8.12	1.12	59
***Cephalophus* spp.**					
Major dry	GLM	7.37 ± 1.16	0.13–39.20	3.25	68
	Arithmetic mean	5.81 ± 0.13	0.13–39.20	2.25	60
Minor wet	GLM	1.52 ± 0.20	0.13–8.00	1.00	101
	Arithmetic mean	1.30 ± 0.02	0.13–8.00	0.25	94
Minor dry	GLM	4.09 ± 0.59	0.25–20.20	1.25	81
	Arithmetic mean	3.75 ± 0.06	0.25–19.20	1.25	77
Major wet	GLM	2.72 ± 0.32	0.13–19.10	1.00	123
	Arithmetic mean	2.05 ± 0.03	0.13–18.00	1.00	110

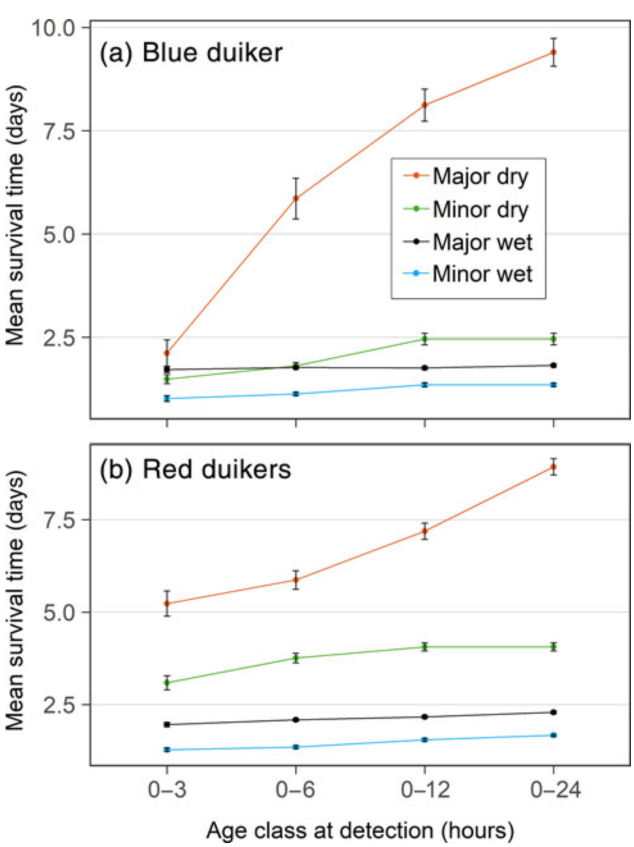

FIG. 2 Mean survival time of dung for different age classes at detection for (a) blue duiker and (b) red duikers in different seasons. Error bars represent 95% confidence intervals.

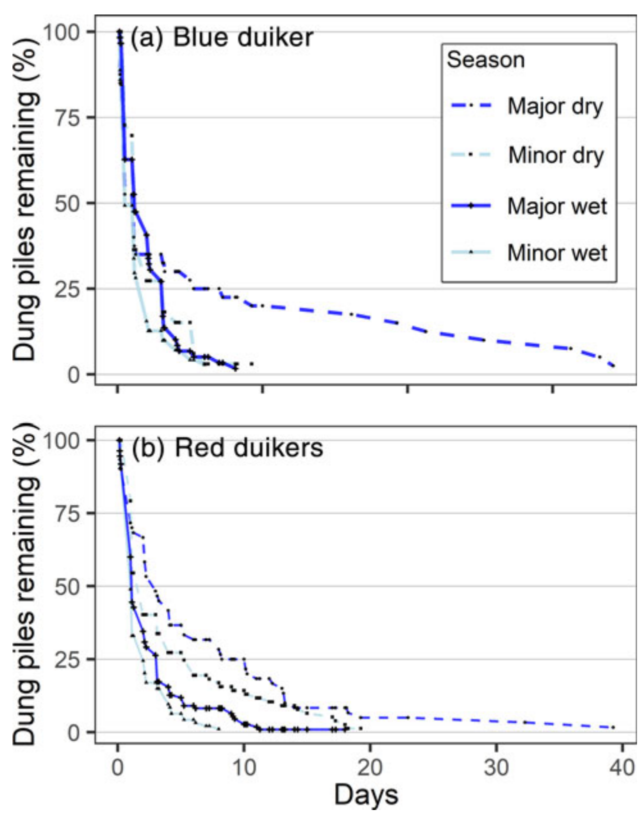

FIG. 3 Survival curve of dung piles of (a) the blue duiker and (b) red duikers in the four seasons.

TABLE 2 Per cent of dung piles of the duikers *P. monticola* and *Cephalophus* spp. disappearing or removed, by cause and season, in Nki National Park, south-east Cameroon.

		% of dung piles disappeared				
Taxon/season	Sample size	Beetles	Leaf cover	Rainfall	Decomposition	Others[1]
Philantomba monticola						
Major dry	50	52.0	18.0	10.0	20.0	
Minor wet	74	78.4	5.4	10.8	5.4	
Minor dry	33	69.8	24.2	3.0	3.0	
Major wet	61	77.1	4.9	8.2	8.2	1.6
***Cephalophus* spp.**						
Major dry	68	48.5	14.7	8.8	26.5	1.5
Minor wet	101	78.2	4.0	6.9	9.9	1.0
Minor dry	81	64.2	7.4	7.4	19.8	1.2
Major wet	123	69.1	2.4	17.9	10.6	

[1]Scattered by birds or trampled by other animals.

negligible as in most cases dung piles were > 10 m apart and we rarely found fresh dung piles within 5 m of each other on the same day.

We conducted all analyses in *R 4.1.0* (R Core Team, 2021). We used a likelihood ratio test to examine individual effects, and we compared the full model with a reduced model lacking the factor to be tested (Barr et al., 2013). We examined the differences between the effects of explanatory variables using t tests. The level of significance was 0.05 for all statistical tests.

Results

We recorded a total of 288 dung piles of the blue duiker and 500 of red duikers, of which 216 and 373 met the final inclusion criteria, respectively (Table 1, Supplementary Table 2). The GLMs confirmed that dung survival time was positively associated with dung age at detection for both the blue duiker (slope coefficient 2.95 ± SE 0.44, $P < 0.001$) and for red duikers (1.87 ± SE 0.33, $P < 0.001$). The effect was strongest in the major dry season. Including dung older than 6 hours at detection resulted in a 4–348% positive bias in estimates of mean survival time for the blue duiker and 4–72% for red duikers (Fig. 2). This implies that dung detected at an older age tended to remain for a longer time than dung detected soon after defaecation (see Discussion). Therefore, to avoid biased estimation, dung piles older than 6 hours at detection were discarded from further analysis.

Overall, 50% of blue duiker dung piles disappeared within 1 day in all seasons, and other dung piles remained for 6–34 days (Table 1, Fig. 3). Similarly, 50% of the dung piles of red duikers disappeared within 1–2.25 days in all seasons, and others persisted for 8–39 days. For both blue duiker and red duikers, dung piles survived for longer in the major dry season.

Most dung disappeared as a result of removal by beetles, leaf cover, rainfall or decomposition (Table 2), with beetles the most important factor for both the blue duiker ($\chi^2 = 25.65$, df = 9, $P < 0.005$) and red duikers ($\chi^2 = 35.81$, df = 9, $P < 0.001$) in all seasons. Overall, 70.6% of dung piles of the blue duiker disappeared as a result of removal by beetles, followed by leaf cover (11.0%), decomposition (9.2%), rainfall (8.7%), and scattering by birds or trampling by other animals (0.5%). Similarly, 66.8% of the dung piles of red duikers disappeared because of beetles, followed by decomposition (15.3%), rainfall (11.0%), leaf cover (6.2%), and scattering by birds or trampling by other animals (0.8%).

Removal by dung beetles contributed the most to shortening dung survival time (Fig. 4, Table 3). The GLMs revealed a significant effect of main factor on dung survival time both for the blue duiker (likelihood ratio test, $D_1 = 120.82$, $P < 0.001$) and red duikers ($D_1 = 225.32$, $P < 0.001$). Season did not have a significant effect for the blue duiker ($D_1 = 7.7$, $P = 0.0502$) and a marginally significant effect for red duikers ($D_1 = 8.4$, $P = 0.0447$). Dung survival time was not correlated with dung pile diameter for either the blue duiker ($D_1 = 0.31$, $P = 0.5729$) or red duikers ($D_1 = 3.7$, $P = 0.0607$). These results mean that the factors causing the disappearance of dung piles, most of which was accounted for by beetle activity, directly affected dung survival time and this was not influenced by dung pile size or season.

Discussion

Our estimates of mean dung survival time (6.83 days in the major dry season and 1.20–1.81 in other seasons for the blue duiker; 7.37 and 1.52–4.09 for red duikers) were substantially shorter than the values commonly used for the estimation of duiker density in Central Africa (i.e. 18 days for the blue duiker, 21 days for red duikers; Koster & Hart, 1988). As shorter dung survival times result in higher estimates of population density, previous studies based on Koster & Hart (1988) are likely to have underestimated duiker densities by an order of magnitude.

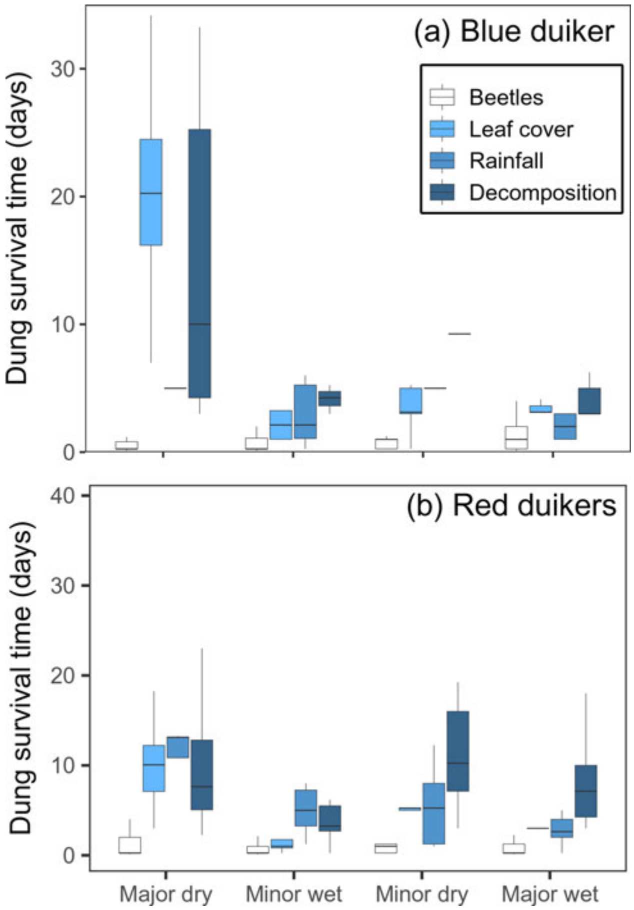

Fig. 4 Distribution of dung survival time for (a) the blue duiker and (b) red duikers by the main factors causing dung to disappear and by season. The horizontal bar and upper and lower box edges indicate the 50, 75 and 25% quantiles, respectively. The whiskers denote 1.5 times the inter-quartile range.

Table 3 Summary of the full and optimal generalized linear models used for testing the effects of factors causing dung to disappear, season and dung pile diameter on dung survival time. Models were fitted with a gamma error distribution.

Explanatory variables	Full model	Optimal model		
	Estimate ± SE	Estimate ± SE	*t*	P
Philantomba monticola				
Intercept	2.01 ± 0.42	2.13 ± 0.25	8.47	< 0.001
Main factor				
Beetles	−2.15 ± 0.26	−2.26 ± 0.27	−8.44	< 0.001
Leaf cover	−0.04 ± 0.34	−0.05 ± 0.35	−0.16	n.s.
Rainfall	−0.75 ± 0.36	−1.00 ± 0.37	−2.69	< 0.001
Season				
Minor wet	−0.47 ± 0.23			
Minor dry	−0.48 ± 0.28			
Major wet	0.01 ± 0.23			
Log(diameter)	0.11 ± 0.17			
***Cephalophus* spp.**				
Intercept	1.81 ± 0.33	2.31 ± 0.19	12.21	< 0.001
Main factor				
Beetles	−2.01 ± 0.17	−2.04 ± 0.16	−12.56	< 0.001
Leaf cover	−0.53 ± 0.30	−0.51 ± 0.30	−1.73	n.s.
Rainfall	−0.69 ± 0.24	−0.67 ± 0.23	−2.92	< 0.005
Season				
Minor wet	−0.51 ± 0.20	−0.39 ± 0.19	−2.07	< 0.05
Minor dry	−0.18 ± 0.22	0.03 ± 0.19	0.16	n.s.
Major wet	−0.20 ± 0.19	−0.08 ± 0.18	−0.49	n.s.
Log(diameter)	0.24 ± 0.13			

Dung beetles, the main factor responsible for the removal of dung piles, preferred fresh dung (Table 2, Fig. 4). In all seasons, dung beetles removed high proportions of fresh dung piles within a few hours of deposition, and other dung piles remained until they disappeared as a result of other factors. This finding is consistent with studies that showed rapid removal of dung by beetles in Gabon (White, 1994; van Vliet et al., 2009) and Congo-Brazzaville (Breuer et al., 2009, 2021) (Supplementary Table 3). As van Vliet et al. (2009) argued, intense beetle activity can consistently hide duikers.

Dung survival time for red duikers and for the blue duiker was up to five and six times longer, respectively, in the major dry season than in the minor wet season. Even within each season, dung survival time was highly variable, ranging from a few hours to ≥ 5 weeks. In Gabon, White (1994) has also noted a wide range of dung survival time for red duikers (up to 2 months) in the dry season.

However, our analysis with GLMs showed that dung survival time was more directly influenced by beetle activity than by season or dung pile size. Therefore, as beetle abundance and activity are likely to vary between regions, the use of dung survival time calculated in a given locality to estimate duiker density in another locality may be inappropriate, even if a dung count survey is carried out in the same season as the estimation of dung survival time. Dung pile diameter had no significant effect on dung survival time, suggesting that beetles removed dung piles independently of their size.

Dung survival time tended to be longer in the major dry season, probably because the proportion of dung piles that beetles removed was significantly lower because of the rapid drying of dung pellets and the low abundance of beetles (Andresen, 1999; van Vliet et al., 2009). Conversely, during wet seasons, beetles were probably more abundant, dung moisture remained high for longer periods and therefore beetles removed dung piles of a wider age range (Fig. 4), resulting in a shorter dung survival time than in dry seasons.

Some previous studies estimated mean survival time of 1–4 days, even in the major dry season (Breuer et al., 2009; van Vliet et al., 2009). Our estimates for mean survival time in the major dry season were higher than this. There are three possible reasons. Firstly, beetles may have been more abundant and active even in the dry season in the areas where these previous studies were carried out, or the forest understorey in south-east Cameroon is dryer than in these other areas. Secondly, we monitored dung piles in natural settings, whereas van Vliet et al. (2009) collected fresh dung pellets from animal intestines and installed the pellets in experimental settings. This method is suitable to measure precise dung survival time but many fresh dung piles deposited simultaneously in a given site could attract more beetles. Thirdly, the rapid removal of dung piles by beetles results in an overestimation of dung survival time, particularly for the major dry season (see below).

The rapid removal of fresh dung piles by beetles has another implication: including dung piles detected when they are older may overestimate dung survival time (Fig. 2). As beetles prefer to remove fresh dung, piles detected at an older age were those that had not been collected by beetles and were likely to remain for a longer time. To minimize this bias and to limit the risk of underestimating duiker densities, we discarded dung piles with an age at detection older than 6 hours from all analyses. Mean and median estimates of survival time of dung detected within 3 hours of deposition were similar to that of dung detected within 6 hours, except for that of the blue duiker in the major dry season. Ideally, therefore, we should have used only dung detected within 3 hours of deposition, but to have a sample size sufficient for analyses we included dung piles detected within 6 hours. Nevertheless, we may have missed some dung piles removed by beetles immediately after deposition. Especially in the dry season, therefore, the proportion of dung piles removed by beetles may be higher than our estimates suggest, which would cause an overestimation of mean dung survival time.

Additionally, the rapid removal of fresh dung by beetles suggests there are interactions between duikers and beetles. Low dung density does not necessarily mean low duiker density. An area containing many duikers is likely to harbour many dung beetles, which remove dung as soon as it is deposited. It is at least possible there are different degrees of abundance and activity of beetles in different habitats. Future studies should therefore investigate dung survival time across habitats, including logged forests.

Our estimate of dung survival time is much shorter (2- to 15-fold for the blue duiker, 2- to 14-fold for red duikers) than values commonly used to convert dung density into duiker population density in Central Africa. Provided that defaecation rates of duikers are comparable between areas, lower values of dung survival time will result in higher estimates of duiker density.

We found the survival time of duiker dung was substantially shortened by beetle activity. The abundance and activity of beetles probably affect the variance of survival time and its seasonality. Ideally, to estimate density of duikers from dung counts, dung survival time should be estimated in the same locality.

The age of dung used to estimate survival time should be considered. Dung decay studies have generally used dung piles up to 1 day old but this may overlook rapid removal of fresh dung by beetles and hence overestimate mean survival time. To minimize the bias that results from this, we recommend that only dung < 3 hours old should be monitored for survival time, with revisits within a few hours and no longer than 1 day. To estimate duiker densities as accurately as possible, surveys of dung survival time should be carried out in the wet season, when variance is lower, and sufficient samples need to be collected for estimation of mean dung survival time and duiker densities.

Acknowledgements This work was supported by the Japan Science and Technology Agency–Japan International Cooperation/Science and Technology Research Partnership for Sustainable Development (Projet Coméca, JPMJSA1702), Japan, and Institute for Agronomic Research and Rural Development, Cameroon. We thank the Ministry of Scientific Research and Innovation and the Ministry of Forestry and Wildlife, Cameroon for granting permission to carry out fieldwork in Nki National Park, the people of the study area for their support during fieldwork, and two anonymous reviewers for their critiques.

Author contributions Study design: TOWK, MT, HY; fieldwork: TOWK, ZCBD, NCBD; data analysis, writing: TOWK, HY.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards, and did not involve collection of animal specimens.

References

Andresen, E. (1999) Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. *Biotropica*, 31, 145.

Barr, D.J., Levy, R., Scheepers, C. & Tily, H.J. (2013) Random effects structure for confirmatory hypothesis testing: keep it maximal. *Journal of Memory and Language*, 68, 255–278.

Beukou, B., Sombambo, M., Nzooh, Z., N'goran, K.P., Hessana, D., Sebogo, L. & Mengamenya, A. (2019) *Dynamique des Populations de Grands et Moyens Mammifères dans le Segment Cameroun du Paysage Tri-National de la Sangha*. Unpublished report. WWF/Sangha Tri-National Foundation/Ministry of Forestry and Wildlife, Yaoundé, Cameroon.

Bobo, K.S., Kamgaing, T.O.W., Kamdoum, E.C. & Dzefack, Z.C.B. (2015) Bushmeat hunting in southeastern Cameroon: magnitude and impact on duikers (*Cephalophus* spp.). *African Study Monographs*, 51, 119–141.

Bobo, K.S., Kamgaing, T.O.W., Ntumwel, B.C., Kagalang, D., Kengne, P.N.J., Ndengue, S.M.L. et al. (2014) Species richness, spatial distributions and densities of large and medium-sized mammals in the northern periphery of Boumba-Bek National Park, southeastern Cameroon. *African Study Monographs*, 49, 91–114.

Bogaerts, K., Komárek, A. & Lesaffre, E. (2018) *Survival Analysis with Interval-Censored Data: A Practical Approach with Examples in R, SAS and BUGS*. CRC Press/Taylor & Francis Group, Boca Raton, USA.

Breuer, T., Breuer-Ndoundou Hockemba, M., Opepa, C.K., Yoga, S. & Mavinga, F.B. (2021) High abundance and large proportion of medium and large duikers in an intact and unhunted afrotropical protected area: insights into monitoring methods. *African Journal of Ecology*, 59, 399–411.

Breuer, T., Mavinga, F.B. & Breuer-Ndoundou Hockemba, M. (2009) Dung decay and its implication for population estimates of duikers (*Cephalophus* and *Philantomba* spp.) and red river hogs (*Potamochaerus porcus*) in the Nouabalé-Ndoki National Park, Republic of Congo: dung decay and its implication for population estimates. *African Journal of Ecology*, 48, 551–554.

Ekobo, A. (1998) *Large Mammals and Vegetation Surveys in the Boumba-Bek and Nki Project Area*. Unpublished report. WWF Cameroon, Yaoundé, Cameroon.

Elenga, G., Bonenfant, C. & Péron, G. (2020) Distance sampling of duikers in the rainforest: dealing with transect avoidance. *PLOS ONE*, 15, e0240049.

Fa, J.E., Peres, C.A. & Meeuwig, J. (2002) Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conservation Biology*, 16, 232–237.

Ichikawa, M. (2014) Forest conservation and Indigenous peoples in the Congo basin: new trends toward reconciliation between global issues and local interest. In *Hunter-gatherers of the Congo Basin: Cultures, Histories, and Biology of African Pygmies* (ed. B.S. Hewlett), pp. 321–342. Transaction, New Brunswick, USA.

Jost Robinson, C.A., Zollner, P.A. & Kpanou, J.B. (2017) Night and day: evaluating transect methodologies to monitor duikers in the Dzanga-Sangha protected areas, Central African Republic. *African Journal of Ecology*, 55, 222–232.

Kamgaing, T.O.W., Bobo, K.S., Djekda, D., Azobou, K.B.V., Hamadjida, B.R., Balangounde, M.Y. et al. (2018) Population density estimates of forest duikers (*Philantomba monticola* & *Cephalophus* spp.) differ greatly between survey methods. *African Journal of Ecology*, 56, 908–916.

Koerner, S.E., Poulsen, J.R., Blanchard, E.J., Okouyi, J. & Clark, C.J. (2017) Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon. *Journal of Applied Ecology*, 54, 805–814.

Koster, S.H. & Hart, J.A. (1988) Methods of estimating ungulate populations in tropical forests. *African Journal of Ecology*, 26, 117–126.

Laing, S.E., Buckland, S.T., Burn, R.W., Lambie, D. & Amphlett, A. (2003) Dung and nest surveys: estimating decay rates. *Journal of Applied Ecology*, 40, 1102–1111.

Letouzey, R. (1985) *Carte Phytogéographique du Cameroun au 1:500000*. Institut de la Recherche Agronomique (Herbier National), Toulouse, France.

Marques, F.F.C., Buckland, S.T., Goffin, D., Dixon, C.E., Borchers, D.L., Mayle, B.A. & Peace, A.J. (2001) Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland: Estimating deer abundance from dung surveys. *Journal of Applied Ecology*, 38, 349–363.

Martin, E.A., Ros Brull, G., Funk, S.M., Luiselli, L., Okale, R. & Fa, J.E. (2020) Wild meat hunting and use by sedentarised Baka pygmies in southeastern Cameroon. *PeerJ*, 8, e9906.

Nzooh Dongmo, Z.L., Ngoran, K.P., Ekodeck, H., Kobla, A.S., Famegni, S., Sombambo, M. & Mengamenya, A. (2016) *Les Populations de Grands et Moyens Mammifères dans le Segment Lobéké et du Tri-National de la Sangha*. Unpublished report. WWF/Sangha Tri-National Foundation/Ministry of Forestry and Wildlife, Yaoundé, Cameroon.

Payne, J.C. (1992) *A field study of techniques for estimating densities of duikers in Korup National Park, Cameroon*. PhD thesis. University of Florida, Gainesville, USA.

Pyhälä, A., Orozco, A.O. & Counsell, S. (2016) *Protected Area in the Congo Basin: Failing both People and Biodiversity?* The Rainforest Foundation, London, UK.

R Core Team (2021) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, J.G., Redford, K.H. & Bennett, E.L. (1999) Wildlife harvest in logged tropical forests. *Science*, 284, 595–596.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L. et al. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, 5–14.

van Vliet, N. & Nasi, R. (2008) Why do models fail to assess properly the sustainability of duiker (*Cephalophus* spp.) hunting in Central Africa? *Oryx*, 42, 392–399.

van Vliet, N., Nasi, R. & Lumaret, J.P. (2009) Factors influencing duiker dung decay in north-east Gabon: are dung beetles hiding duikers? *African Journal of Ecology*, 47, 40–47.

Viquerat, S., Bobo, K.S., Kiffner, C. & Waltert, M. (2013) A comparison of regression-based estimates of dung decay in two African forest duiker species. *Ecotropica*, 19, 33–38.

White, L.J.T. (1994) Biomass of rain forest mammals in the lope reserve, Gabon. *The Journal of Animal Ecology*, 63, 499.

White, L. & Edwards, A. (eds) (2000) *Conservation Research in the African Rain Forests: A Technical Handbook*. Wildlife Conservation Society, New York, USA.

Wilkie, D.S. & Carpenter, J.F. (1999) Bushmeat hunting in the Congo basin: an assessment of impacts and options for mitigation. *Biodiversity and Conservation*, 8, 927–955.

Wilkie, D.S. & Finn, J.T. (1990) Slash–burn cultivation and mammal abundance in the Ituri Forest, Zaire. *Biotropica*, 22, 90.

Yasuoka, H. (2006) The sustainability of duiker (*Cephalophus* spp.) hunting for the Baka hunter-gatherers in southeastern Cameroon. *African Study Monographs*, 33, 95–120.

Yasuoka, H., Hirai, M., Kamgaing, T.O.W., Dzefack, Z.C.B., Kamdoum, E.C. & Bobo, K.S. (2015) Changes in the composition of hunting catches in southeastern Cameroon: a promising approach for collaborative wildlife management between ecologists and local hunters. *Ecology and Society*, 20, 25.