

Ageing of ungulate pellets in semi-arid landscapes: how the shade of colour can refine pellet-group counts

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Abstract Pellet-group counts can be useful in monitoring ungulate population trends, particularly in elusive species. In semi-arid areas, ambient conditions conserve the pellets during the dry season. Thus, dating of accumulated pellet groups should be helpful in approximating the numbers of ungulates present during any chosen part of the dry season. The aims of this study were to confirm that the decay rate of pellet groups was low during the dry season, to identify the major causes of decay and to test the usefulness of criteria, easily measurable in the field, in dating pellets. Every month during the dry season pellet groups of five African savanna ungulates were collected fresh and deposited on bare ground at an experimental site. The levels of hardness, cracking, scattering, attack by insects and shade of colour of the pellets were monitored until the rainy season started. As expected, only a few pellet

groups decayed completely during the dry season. The pellets' shade of colour was the best criterion to date them. We discuss pellet colour as an original tool for monitoring the trends in ungulate use of target areas in semi-arid environments.

Keywords Africa · Faecal pellet · Indirect surveys · Population monitoring · Savanna

Introduction

The sustainable management of wildlife populations in conservation areas, as well as in rangelands, strongly depends on the monitoring of population status and spatio-temporal trends (e.g. Kremen et al. 1994; Yoccoz et

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al. 2001; Gordon et al. 2004). Many techniques have been employed to monitor large terrestrial mammal populations (e.g. see review by Van Hensbergen and White 1995; Morellet et al. 2007), including the use of indirect indices, especially for elusive species or in dense habitat (Stephens et al. 2006). Pellet-group counting can provide an objective measure of population fluctuations (Marques et al. 2001; Campbell et al. 2004), and can also aid in describing distribution, habitat preference and seasonal changes in patterns of habitat use (Putman 1984). This approach, mainly developed in ungulates in temperate or arid regions in America or Europe (e.g. Mayle and Peace 1999; Acevedo et al. 2010), has now begun to be used to monitor African ungulate populations (e.g. Plumpré 2000; Barnes 2001; Ellis and Bernard 2005). Still, research is needed to adapt these techniques to tropical areas with their specific animal diet and climatic conditions.

In semi-arid ecosystems such as tropical savannas, very dry conditions during the aptly called dry season may lead to good preservation of pellet (Jachmann and Bell 1979, 1984). Conversely, pellet groups are assumed to decay rapidly during the rainy season. Pellet-group counts following a ‘standing crop procedure’ during the dry season (Putman 1984; Mayle and Peace 1999) would give a simple estimation of mean animal number in the area since pellets start to accumulate without destruction, i.e. after the last rains and possibly management fires at the beginning of the dry season. However, these critical dates may fluctuate from year to year, and one must be very careful to guarantee similar periods (same length) before making inter-annual comparison of animal abundance estimates resulting from a ‘standing crop procedure’. Furthermore, if the counting can be carried out at any time during the dry season, this procedure implies that the period considered necessarily stretches back to the beginning of the dry season. A ‘clearance plot’ procedure (Mayle and Peace 1999) would thus appear as an interesting solution to focus counting on a chosen period of the dry season that best fits with a homogeneous use of the area by the ungulate population studied. However, this method might be excessively time consuming as it requires a prior sampling and clearing effort over sufficiently large sampling areas to detect pellet groups.

We propose an alternative approach based on the ability to estimate the age of pellet groups. This consists in conducting a single count using a ‘standing crop’ procedure, but also in identifying the age of the pellets in order to consider only the pellet groups deposited over the target period. To our knowledge, very few studies have used or investigated the dating of pellets to refine population monitoring in semi-arid environments. Neff (1968) suggested that the shape and shade of pellets could be correlated with seasonal changes in diet. Young et al.

(2005) and Sullivan et al. (2002) also used the pellet shade, as well as odour and cracking, as indicators of pellet transformation over time, in zebra and koala respectively. In this study, we characterized the decay and ageing processes of pellets along the dry season until the beginning of the rainy season in a savanna ecosystem. We worked on faeces of five ungulates of various sizes and feeding styles living in the Niger W Regional Park in West Africa. After having verified the effect of dry and rainy conditions on pellet-group decay, we studied whether simple and reliable criteria could be identified to age faeces during the dry season. We particularly tested the relevance of the colour shade criteria and as well other criteria easily measurable in the field. We finally discuss how pellet dating could be used to monitor ungulate populations in semi-arid biomes.

Materials and methods

Study area

The W Regional Park (WRP) (N 11°30', E 1°30') comprises three contiguous National Parks, crossing the borders between Benin (550,000 ha), Burkina Faso (250,000 ha) and Niger (220,000 ha). The area exhibits the Sahelo–Sudanian climatic conditions typically found along a wide strip bordering the southern Sahara. The annual rainfall, although averaging between 600 mm in the north and 1,000 mm in the south, is very erratic and restricted to the well marked rainy season (from May/June to September/October). The predominant vegetation type is Sudanese wooded savanna.

Field data collection

The study of faeces decay was carried out during the dry season from December 2004 to June 2005, until the first heavy rains, in the northern part of the WRP. We studied pellet-group degradation in species producing pellets of various sizes and compositions owing to differences in diet. We focused on four mainly grazing species whose body mass values were taken from the local field guide of Lamarque (2004): the Bohor reedbuck (*Redunca redunca* Pallas, 1767) (48 kg), Buffon’s kob (*Kobus kob* Erxleben, 1777) (76 kg), the Defassa waterbuck (*Kobus ellipsiprymnus defassa* Ogilby, 1833) (200 kg), the roan antelope (*Hippotragus equinus*) (265 kg), and on one mixed-feeding species: the red-fronted gazelle (*Gazella rufifrons* Gray, 1846) (28 kg). Waterbuck and roan antelope have also been described to incorporate non-negligible amounts of browse in their diet at the end of the dry season (Schuette et al. 1998; Kassa et al. 2007).

Each month and for each species, we collected about ten (from four up to 14) fresh pellet groups from different locations of the Park. Each was placed in a different and new 50×50 cm square plot on bare ground marked out by stones in a bush savanna area. This resulted in building as many square plots as collected pellet groups (total per species given in Table 2). Half the collected pellet groups were deposited in plots in the shade of trees and the other pellet groups were deposited in plots in full sunshine in a clearing on the experimental site. Thus, our design produced several spatial replicates for a same species and same month of collection for homogenous environmental conditions, i.e. in the shade or exposed to sun, and accounted for the inter-individual variability in the temporal transformation of pellet groups. In order to allow comparison of the changes occurring in the pellet groups placed in different plots in both exposure situations, we limited the faecal matter per pellet group to the same arbitrary fixed quantity of about 30 pellets.

Measurements

Every 2 weeks, we checked whether each pellet group was still present or had completely decayed. We considered the pellet group as decayed when less than four pellets remained in the square plot. We measured different characteristics of the pellet groups in order to describe the ageing process and to investigate the causes of decay.

Since we observed that all pellet groups freshly defecated by animals were dark, we assumed that paler pellet groups should be older than dark ones. To investigate the relationship between the colour of pellets and the pellet-group age, we described the colour shade with four contrasting classes (Fig. 1, Table 1). Although the classification by naked eye was admittedly quite subjective, these classes were distinguished in the same manner and systematically recognized by several experimenters. All persons tested ($n=3$ and 5 or more repetitions) and classed all the pellets in the same four categories. We also looked for other criteria easily measurable in the field that may indicate pellet ageing linked to the desiccation process. We observed that some pellet groups presented cracked pellets and that pellets could appear either soft, very hard or brittle

when pressed between fingers. We recorded the level of pellet cracking and of pellet hardness in four main classes as well (Table 1) to test whether these simple field measurements could be useful for dating pellet groups. At each visit, we observed that all pellets of one pellet group showed consistent evolution (same levels) in terms of shade, cracking and hardness. Thus, there was no hesitation in attributing a class to pellet group that would have been the case with pellets in different states within a same pellet group.

The pellet groups had been transported and were not in their initial scattering state, but we wanted to get an idea of how much the scattering factor could participate in the disappearance of a pellet group. In all plots, pellets were gathered together in the same standardised way at the centre of the plot and then remained untouched. We identified two other processes of decay: (1) natural embrittlement due to extended desiccation leading to pellets breakdown and (2) degradation by insects. Pellets attacked by insects appeared to be cropped and perforated and sometimes cemented when attacked by termites. Hence, we clearly distinguished between situations where pellet groups decayed following gradual degradation of pellets by insects (clear marks and sometimes direct observations of insects) and situations where pellets scattered or crumbled without being attacked by insects (surface intact except for cracks).

Analysis

The initial state of the fresh pellet group (intact pellets gathered in the middle of the plot) served as the reference state at the beginning of our longitudinal survey. The process of pellet-group ageing and decay was analysed through the temporal evolution of the measured variables, i.e. shade of colour, cracking, hardness, scattering and degradation by insects, and the proportion of remaining pellet groups.

For each species, we looked for the variable that best indicated the age of the pellet groups. We do not advise using pellet scattering to date pellet groups in the field since we never know their initial level of scattering. Neither can we use the level of degradation by insects in natural conditions without any knowledge about the pellets already degraded by insects. Due to repeated measurements on the same pellet

Fig. 1 Buffon's kob pellets ranging from dark and fresh (colour shade class A) to lighter and older (class D)

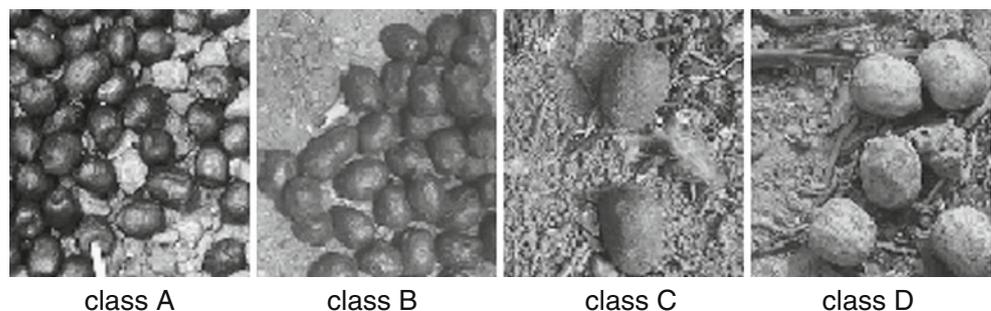


Table 1 Definition of classes of variables used to characterize pellet-group ageing

Class code	Criteria				
	Colour shade of pellets	Cracking of pellets	Hardness of pellets	Scattering of the pellet group	Degradation of the pellet group by insects
A	Dark and wet, with a glossy patina	Smooth surface	Very soft	Not scattered	No pellet with marks of attack
B	Dark but dry on surface, without patina	Light cracking thinner than a hair	Resistant but can be mushed between fingers	<10% pellets scattered	<10% pellets attacked
C	Dull	Wider cracks (<1 mm wide)	Very hard, cannot be mushed between fingers	>60% pellets scattered	>60% pellets attacked
D	Very dull and light greyish	Deep splits (≥ 1 mm wide)	Brittle	<10% pellets remaining ^a	<10% pellets remaining ^b

Attack by insects was assessed by consumption and degradation traces on the pellets.

^a Knowing that more than 60% of pellets of the pellet group were previously (last checking scattered; i.e. in state C)

^b Knowing that most pellets (>60%) of the pellet group previously exhibited marks of attacks by insect (state C)

groups, individual pellet groups were expected to generate non-independent estimates of age. Therefore, we used a linear mixed model approach to account for random effects of pellet group (Zuur et al. 2009). We fitted age linear mixed models independently on colour, cracking and hardness using the *lmer* function of the *lme4* library (Bates and Maechler 2010) of the R 2.7.1 software (R Development Core Team 2008). These variables were fitted as a fixed effect and the pellet group identity as a random effect, considering a normal distribution of the untransformed (identity link) response variable, i.e. the pellet-group age. We selected the variable corresponding to the model that best fitted the observed data. The fit of models was measured by the proportion of the explained variance calculated as the square of the correlation coefficient (i.e. coefficient of determination R^2) between the predicted and the observed ages.

Then, we tested the effect of exposure on pellet-group age, i.e. we tested whether the classes of the selected

variable were reached earlier (or later) by pellet groups in full direct sunlight than by pellet groups shaded by trees. For each species, we compared the age linear mixed model including the selected variable with the age linear mixed model including both the selected variable and the exposure factor. The change in deviance between the two models due to the additive effect of exposure was tested against a χ^2 distribution. All analyses were performed using the R 2.7.1 software (R Development Core Team 2008).

Results

Pellet-group ageing and decay during the dry season

As expected, in the five species studied, we recorded a very low decay rate (less than 15%) during the dry season (Table 2). Most decayed pellet groups disappeared because

Table 2 Decay rate and observed causes of pellet disappearance during the dry season, between December and May

Species	Pellet groups				Reasons of total decay				
	Total number	Attacked by insects (%)	Completely decayed (%)	Mean monthly decay rate (\pm SD) (%)	Insects only (%)	Insects + scattering (%)	Scattering only (%)	Scattering + embrittlement (%)	Embrittlement only (%)
Red-fronted gazelle	50	14	10	2 \pm 4	40	20	20	20	–
Roan antelope	50	22	14	4 \pm 6	63	25	–	12	–
Defassa waterbuck	61	31	4	1 \pm 1	100	–	–	–	–
Buffon's kob	53	28	8	1 \pm 2	100	–	–	–	–
Bohor reedbuck	40	40	2	0 \pm 1	–	–	–	–	100

The mean monthly decay rate for the dry season was calculated on the basis of decay rates of different cohorts weighted by the number of months. The definition of a cohort we used was a set of pellet groups collected and deposited on the experimental site in the same month

of degradation by insects, principally termites and ants, except for Bohor reedduck droppings, which were never attacked by insects, but degradation by insects did not necessarily lead to total decay. A small proportion of red-fronted gazelle and roan antelope pellet groups also decayed because of complete scattering (Table 2). Between 8% and 10% of total pellet groups in each species reached a high scattering level (D), after more than 3 months. Two small sporadic bouts of rains (3–4 mm) occurring during the dry season in March and April, made pellets globally more cracked, less hard and more crumbly, more obviously so in red-fronted gazelle. For none of the species, did we find a statistical difference between the proportions of decayed pellets located in the sun and those located in the shade (Fisher's unilateral test, $p > 0.172$ in each species).

As soon as the first heavy rains fell in June, almost all pellet groups finally decayed completely. They were dispersed and washed away by run-off or degraded and covered over by seedling vegetation.

Selection of criteria to estimate pellet-group age

Age model selection showed that the shade of colour appeared to be the most useful criterion for dating pellets in all studied species (Table 3). Softness was only useful to identify pellets aged less than 1 day. Beyond 1 day, pellets were already of maximal recorded hardness (class C) and remained so for up to several months.

The exposure to the sun had no significant effect on the pellet colour in any species (tests of change in deviance

Table 3 Comparison of candidate linear mixed models for pellet-group age in the five ungulate species studied

Species	Model	Deviance	R^2
Red-fronted gazelle	Colour	4,258.48	0.70
	Hardness	4,468.35	0.54
	Cracking	4,481.38	0.48
Roan antelope	Colour	4,030.02	0.79
	Cracking	4,248.51	0.70
	Hardness	4,501.79	0.42
Defassa waterbuck	Colour	6,039.53	0.64
	Cracking	6,225.29	0.52
	Hardness	6,362.70	0.37
Buffon's kob	Colour	5,147.81	0.78
	Hardness	5,633.51	0.48
	Cracking	5,691.97	0.40
Bohor reedduck	Colour	3,159.88	0.79
	Hardness	3,267.92	0.73
	Cracking	3,528.58	0.48

The highest R^2 values, calculated as the correlation between predicted and observed data values, indicate the best fitted models on observed data

between the model with and the model without the exposure factor: $p > 0.168$) except in Buffon's kob ($p = 0.005$). In this species, pellets appeared to become dull more quickly when exposed to the sun (colour class reached on average 10.7 ± 3.8 (SE) days earlier). Colour shade also presented bias due to rainfall. The exceptional light rains during the dry season washed off the dust deposited by the Harmattan winds. This resulted in a momentary change in the shade of colour by one class level, i.e. to shinier but darker shade than previously. Nevertheless, in less than 2 weeks, they tended to return to their original colour levels and beyond.

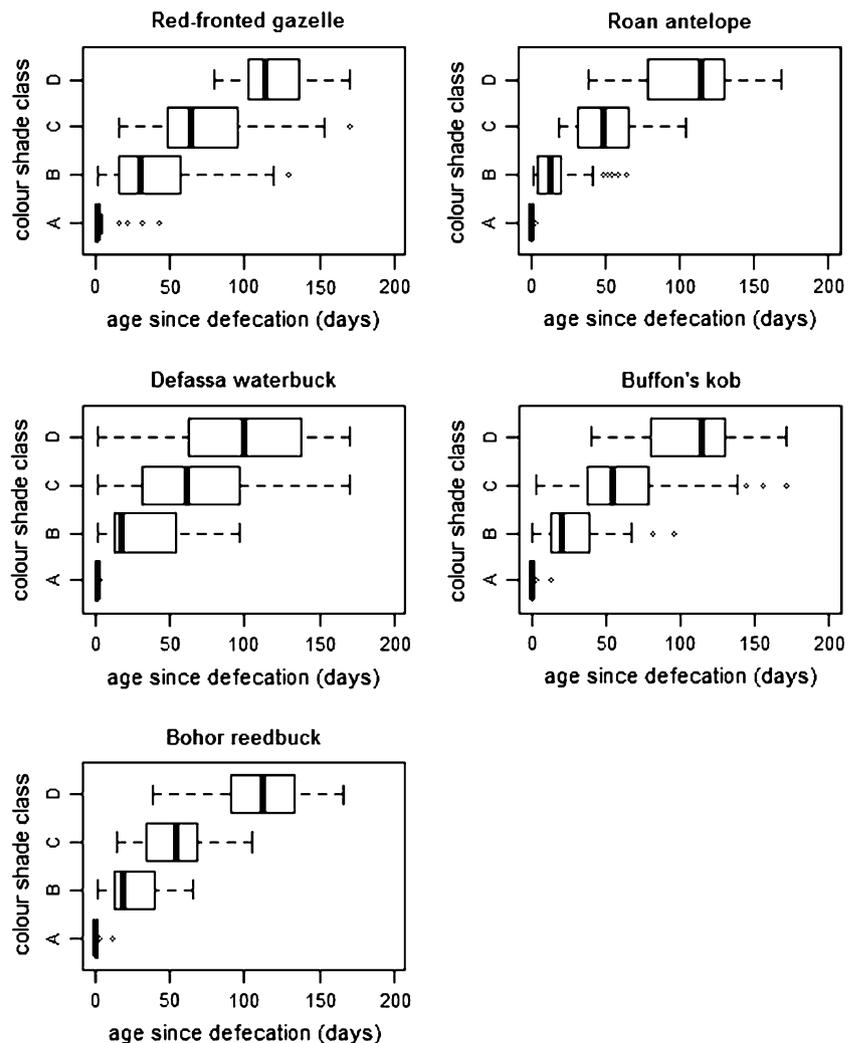
Finally, dating by shade of colour appeared to be most reliable and precise in roan antelope, Buffon's kob and Bohor reedduck whose blackish pellets got steadily duller (Fig. 2). In waterbuck, we were able to age very fresh pellets correctly but it was not so easy with older pellets since even relatively fresh pellets rapidly become very dull in that species. Our colour shade classification proved less straightforward to read with clearer and brownish pellets such as those of the red-fronted gazelle. Pellet cracking and hardness appeared much less reliable except in roan antelope and Bohor reedduck respectively.

Discussion

The trends in the decay and ageing of pellet groups were overall quite similar in the five ungulates studied although they differed in size and feeding style. Pellet lifetime was confirmed to be short and rain-dependent during the rainy season. Thus, we do not recommend pellet-group counts during periods of regular rain. On the other hand, pellet-group decay appeared very low during the dry season, as noted by Jachmann and Bell (1979, 1984) in Southern African savannas.

Although our experimental site was located in one of the predominant habitat of the Park, we acknowledge that it might not be representative enough to account for differential decay that might occur in different habitat conditions of the Park (see Marques et al. 2001; Tsaparis et al. 2009). This may explain why we did not observe any dung beetle attack on the pellets in the experiment site whereas typical attacks were noted in other areas of the Park at the very end of the dry season. Another explanation might be that our site was located in the North of the Park where monsoon front arrived a few weeks later than in the rest of the Park. Studies in other savanna regions (e.g. Krell et al. 2003) confirmed that dung beetle activity and subsequent pellet degradation are maximal during the rainy season and minimal during the dry season, as we observed. We may have concluded our experiment before dung beetles started to be active at this latitude. In contrast,

Fig. 2 Box-and-whisker plots showing lifetime of colour shade classes of monitored pellets during the dry season. The bold line within the boxes represents the median

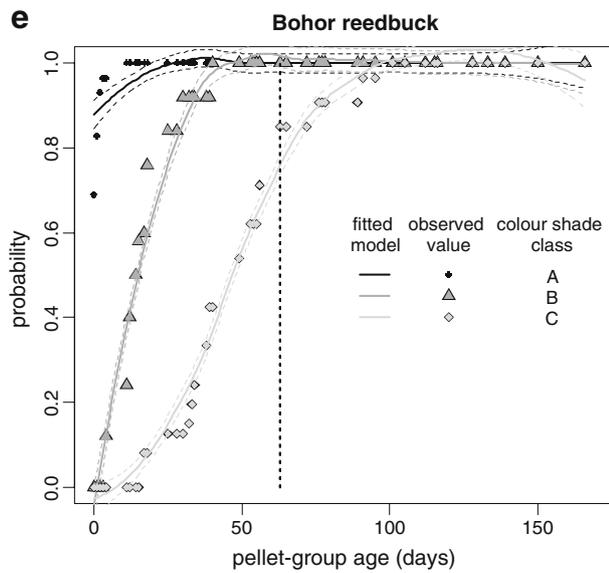
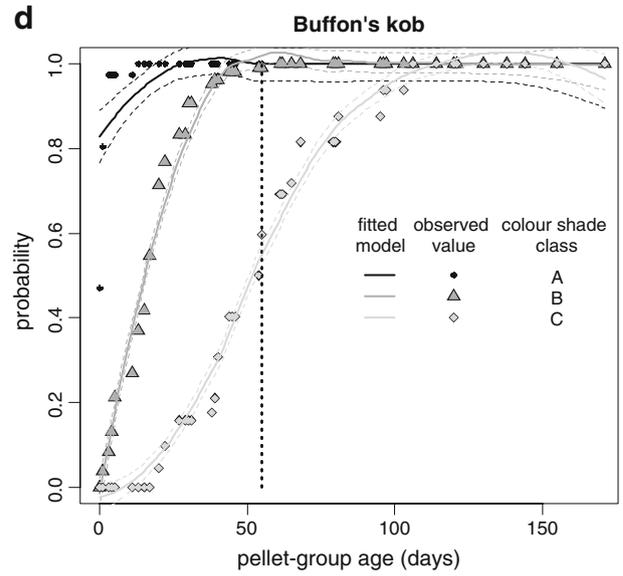
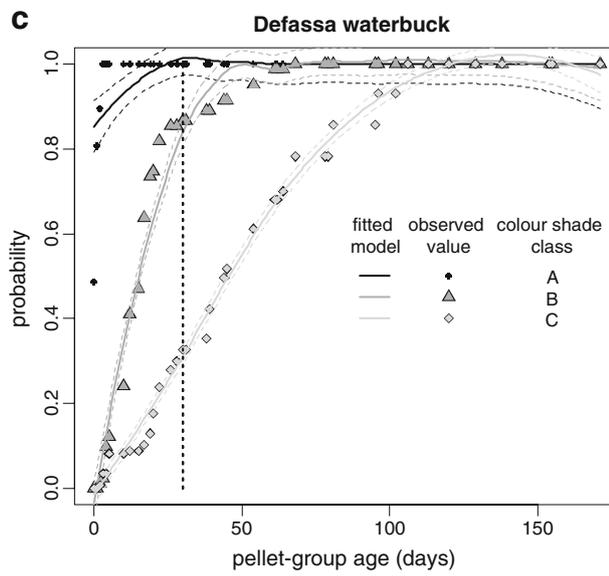
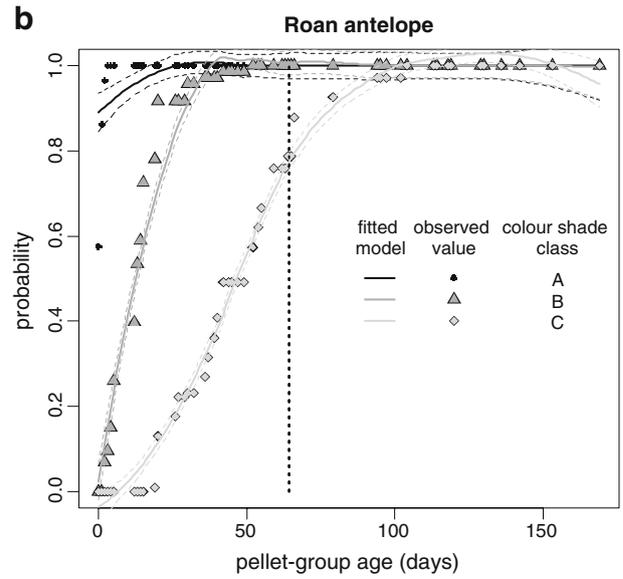
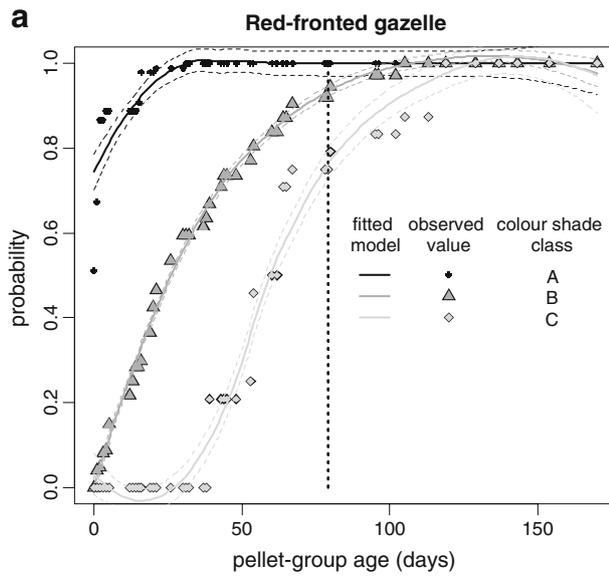


concentrating the pellet groups in the same area might have attracted termites. This could well have led to an overestimation of termite influence on pellet decay rate for the whole dry season. Under natural conditions, pellet groups might initially be more dispersed than in our experiment, and might decay more rapidly because of the scattering. Scattering, however, appeared to be a slow phenomenon on bare soil.

Before the end of the dry season and the concomitant appearance of the dung beetle, we can reasonably think that overall pellet decay is low but the probability that a pellet group will decay increases with the time since defecation (Laing et al. 2003). In order to limit the uncertainty on the initial number of pellet groups deposited due to decay and to temporal variation of defecation rates (Macracken and Ballenberghe 1987; Rogers 1987) and for the reasons explained in the Introduction section (e.g. natural fluctuations, fires, etc.), it may be interesting to focus on monitoring of ungulate populations on a shorter period of time than the whole dry

season. In the five species tested, we found the colour shade of the pellet group to be the most reliable age criterion easily measurable in the field. As observed by Sullivan et al. (2002) in koalas, the more the pellets are cracked the older they are too. Nevertheless, neither

Fig. 3 The probability that the age attributed to a pellet group of a given colour shade is lower than or equal to the actual age: **a** in the red-fronted gazelle, **b** in the roan antelope, **c** in the Defassa waterbuck, **d** in Buffon's kob and **e** in the Bohor reedbuck. This probability was derived from the observed proportions of pellet groups of a given colour shade younger than or the same age as to the considered ages. For each colour shade, we only considered the pellet groups that had had the time to pass to the following shade class in order to prevent a distribution skew due to the experiment design. When some pellet groups passed to a lower shade class (darker) after a light rain, we kept the previous level, to approximate the profile in the event of no rain. Less than 5% of pellet groups of colour shade of class D had an age lower than the value indicated by the vertical dashed line. Other lines represent polynomial models fitted on the observed values using local fitting with the Loess function of the R software Stats package to illustrate the trends. Confidence intervals around predicted values were built by using the *predict* function of the same package



cracking nor hardness were as good predictors of pellet age as the colour shade. Other criteria such as the odour of pellets could also be tested in ungulates but odour may vary much more between individuals feeding on diverse items than in koalas feeding exclusively on fragrant eucalyptus.

The colour of the pellets may change according to the diet of the animal but globally on our samples, the colour shade was a useful age indicator although observer subjectivity to attribute a shade class by naked eye may have brought noise in our data. We may facilitate the attribution of a shade class by naked eye by referring to printed shade charts presenting our reference classes, as carried out by Sullivan et al. (2002). To guarantee more standardized measurement, we could also use an automatic measurement procedure such as computer-assisted analysis of the distribution of grey values of black and white photographs of pellet groups taken in controlled-light conditions. Nevertheless, the information gained with this procedure should be evaluated with regard to its applicability in the field on large spatial and temporal scales by a follow-up study of financial and time costs and facility of implementation.

Perspectives for population monitoring

The number of pellet groups actually deposited for a given period could be approximated as the number of pellet groups of one or several shade classes being indicative of the period. However, the way that an age class is attributed to a shade class and the way a shade class is attributed to an age class, produces an uncertainty on the estimated number of pellet groups deposited over a considered period (Fig. 2). Nevertheless, we can assume that the rate of change of the pellets shade is similar from year to year and as would the systematic uncertainty on the estimate of pellet-group number.

Another approach could consist in estimating the number of pellet groups deposited over a given time interval, using the probability that a pellet group of a given shade class is deposited during that period of time. Let N_x be the number of pellet groups actually deposited by the target population for x days preceding the day of counting and counted on the transects and N_{ci} the number of counted pellet groups of shade ci . Among the N_{ci} pellets, a certain proportion $P_{ci}(x)$ are from the N_x pellets, the others being older than x days. The proportion $P_{ci}(x)$ can be estimated by the probability that the age of the pellet group of shade ci is lower than or equal to x (Fig. 3). If the proportion of pellet groups that decayed during period x is trivial, N_x can be approached by: $\hat{N}_x = \sum N_{ci} \times P_{ci}(x)$. Since it is difficult to approach the real profile of the probability for class D in the absence of measurements for the whole dry season, we can restrict the

study to periods such that x is lower than the time for the first D to appear and then consider $P_D = 0$.

If the decay rate is also known according to pellet-group age and period of the year, the number of deposited pellet groups and hence the apparent density of animals could be theoretically estimated from sample counts. Line transect procedures as described by Marques et al. (2001) (used e.g. in kudu, Ellis and Bernard 2005) might be interesting but very time consuming. Precise measurement of pellet group distances from the axis of the transect are needed. Many transects should also be travelled to guarantee a sufficient minimum number of observations in the case of low densities. A design simpler than line transects would consist in strip transects crossing all types of habitats and on which it is assumed that no pellet groups are undetected (Acevedo et al. 2008). Strip transects 1–2 m wide (or less according to pellet-group detectability) could be covered in a single sweep from one end to the other (Buckland et al. 1993; Acevedo et al. 2010).

Furthermore, wildlife managers nowadays tend to base their management and conservation decisions on population history and fluctuation over time through trend indices rather than punctual densities (see Morellet et al. 2007). The kilometric index (Vincent et al. 1991; Maillard et al. 2001), for example, is basically calculated as the number of animals encountered per kilometre of fixed circuits but could be adapted to indirect indices. Specific kilometric indices could be based on the number of pellet groups of certain shades corresponding to specific age classes. If the defecation rate is not too variable, these indices should indicate the population trends over the years in the target area. Alternatively, a kilometric index of pellet groups deposited for a time interval x could also be derived from our second approach: $IK_x = \hat{N}_x/L$, where L is the transect length. A set of several transects could be travelled simultaneously in order to take account of the spatial heterogeneity of the pellet-group distribution due to animal movements. The mean of indices calculated on individual transects would then provide a yearly, robust indicator of the pellet-groups' overall abundance over the area considered for the same time interval x . Meanwhile, further experimental studies using known population abundance should be conducted to validate the usefulness of this index as a reliable indicator of population trends.

Each year, pellet group counts should be conducted at periods when environmental conditions are similar and along the same fixed circuits. In order to limit uncertainty on decay rates due to coprophagous beetles, or uncertainty on pellet-group age due to alteration of shade by rain, we recommend that pellet-group count be performed before March in West African savannas. During this period, generally no rain occurs and beetle activity is at its lowest. The annual pellet-group count could be performed within a

few kilometres of water points where most savanna ungulate species concentrate during the dry season (Western 1975). We feel that our approach should also be tested and may be extended to other herbivore groups living in environments undergoing regular periods of dry conditions.

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