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RESEARCH ARTICLE

Age-Specific differences in Asian elephant defecation, dung decay, detection and their implication for dung count

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Abstract

1. In vertebrate population estimation, converting faecal density into animal density requires information on the faecal production rate, decay rate and faecal density. Differences in the above factors for long-lived species across age classes were not evaluated. We have evaluated these factors associated with the dung count of Asian elephants (*Elephas maximus*) in the tropical forest of southern India.
2. The defecation rate of elephants was determined in semi-wild elephants at the Mudumalai elephant camp. The relationship between dung bolus diameter and age was determined to estimate the age of the elephant. The total and age-specific elephant density based on dung bolus diameter was estimated. A total of 24 transect lines of 2–4 km (125 km) were sampled in the study area. An experiment was conducted to assess the detection probability across the age classes of dung piles. The dung decay rates across age classes and seasons were determined by marking fresh dung piles ($n = 1551$). The dung-based age structure assessment and its limitations were evaluated.
3. The mean defecation rate was 13.51 ± 0.51 per day. The defecation rate was significantly lower for the younger age class and increased with the age of elephants. Defecation rates were significantly lower in the wet season than in the dry. The dung bolus diameter positively increased with the age of elephants, and the growth curve can be used to predict the age and age structure of elephant populations.
4. The disparity in the dung production rate results in the lower availability of younger age class (juvenile and calf) dung in the transect for counting, which results in lower dung abundance. The detection probability of dung piles of younger age classes was low (0.58). The survival rates of dung piles of younger age classes were lower and increased with the age of elephants in the wet season. Hence, the demographic assessment of the population based on dung needs to consider age-specific differences in dung production, decay and detection probability. Although the

demographic assessment using dung provides insight into population age structure, it has limitations in predicting age structure for young elephants.

KEYWORDS
Asian elephant, decay rate, defecation rate, dung count, growth curve, population estimation

1 | INTRODUCTION

Estimation of wildlife population with precision and accuracy is essential in wildlife management (Williams et al., 2002). Population density and age structure are essential for understanding the population biology of species. Estimating proper density and age composition is essential for assessing the impact of poaching, habitat management and population management of endangered species (Riddle et al., 2010). The Asian elephant (*Elephas maximus*) is listed as an endangered species due to a decline in the population of over 50% in the past three generations. India holds 60% of the Asian elephant population with an estimated population size of 29,964 (Williams et al., 2020) and is being threatened by habitat degradation, conflict and poaching (Riddle et al., 2010; Sukumar, 1989).

Both in Africa and Asia, elephant populations have been estimated using direct count (Dawson, 1990; Daniel et al., 2008; Goswami et al., 2019; Varman & Sukumar, 1995), aerial surveys (Norton-Griffiths, 1978) and indirect count methods (Barnes et al., 1995; Merz, 1986; Oliver et al., 2009). The direct count method requires adequate spatial and temporal replication, a shorter sampling time to ensure population closure and an adequate number of detections to increase precision (Buckland et al., 2001; Jathanna et al., 2015). Dung count provides a more precise estimate than other methods because it records the accumulated presence of animals, variation among the transects is less (Barnes, 2001) and more detection helps in better model fit in the distance sampling. In addition, the cost involved in the survey, field equipment and field training requirements for volunteers is low. Further, the variance caused by defecation and decay rates is moderate (Barnes, 2001). Both the defecation and dung survival rates were used as denominations in the density estimation, which is exponentially related to dung density. When compared to the dung density, the numerical values of both these variables are lower and hence the variability within these factors results in less variance in the final estimate.

Population estimation based on dung count requires estimates of dung density, the dung production rate and the rate at which dung piles decay (Barnes & Jensen, 1987; Dawson & Dekker, 1992; Wing & Buss, 1970). However, studies using this method to estimate populations are seldom estimated for specific sites and were borrowed from other studies that failed to fully capture their inherently high spatio-temporal and age-sex class variations. This can result in a substantially biased estimate of elephant density, which has been highlighted in previous studies (Barnes et al., 1997). We have estimated the defecation rate and dung decay rate in the southern Indian population of elephants, which can be used for estimating elephant density. In India, in addition to the direct count method, the elephant population has been estimated based on the indirect dung count method as part of elephant population monitoring work through the 'Synchronized Elephant Census' in the elephant range states (Bist, 2003; Rangarajan et al., 2010). Therefore, it is essential to evaluate the parameters of the dung count to suggest a proper estimation protocol.

The reported defecation rate for Asian elephants ranges between 9.3 and 15.9/day (Dawson, 1990), which is less than African elephants (19.8/day; Tchamba, 1992). A number of studies have reported seasonal, habitat, regional and interannual variations in the defecation rate (Dawson, 1990; Nchanji et al., 2008; Wing & Buss, 1970). In earlier studies, the defecation rate was assumed to be constant across age classes, and there was no reported age-specific difference in defecation rate in elephants that could potentially influence density estimates. Further age structure estimation based on dung measurements was also biased towards adults (Oliver et al., 2009; Reilly, 2002) and was speculated to be due to differences in defecation, detection and decay rates (Hema et al., 2017). The elephant is a long-lived species and requires 10–15 years to reach sexual maturity, and there is greater variation in body size across age classes (Sukumar, 1989). Hence, it is essential to estimate the defecation rate across age classes and incorporate these differences in the density estimate.

Another important aspect of distance sampling is the detection probability. There are few studies on detection probability. Studies on point counts of birds for detection probabilities using a two-observer sampling method improved the detection and precision of the estimate (Nichols et al., 2000). Estimating the factors that determine the detection probability and incorporating them into the analysis is essential to increase the precision of the estimate.

The design and experimentation on robust estimation of decay rate have received little attention, and decay rates were more often used from other sites. A site-specific variation in decay rate was reported (Barnes & Barnes, 1992; Nchanji & Plumptre, 2001). White (1995) reported differences in decay across months. Earlier estimates of the decay rate were based on the prospective method. Marques et al. (2001) and Laing et al. (2003) proposed a retrospective approach to estimate decay rates that estimate the mean life span of dung piles found at the time of the survey. We estimated seasonal and age-specific variation in the dung decay rate.

It has long been recognized that age-structure data contain useful information for assessing the status and dynamics of wildlife populations (Caughley, 1977; Williams et al., 2002). Assigning age estimates can be difficult if the study organism is large and has a long lifespan. Birth registration and individual recognition are the only methods of assigning exact ages, which may require a longer duration for surveying a larger fraction of the population (Moss, 2001). As an indirect

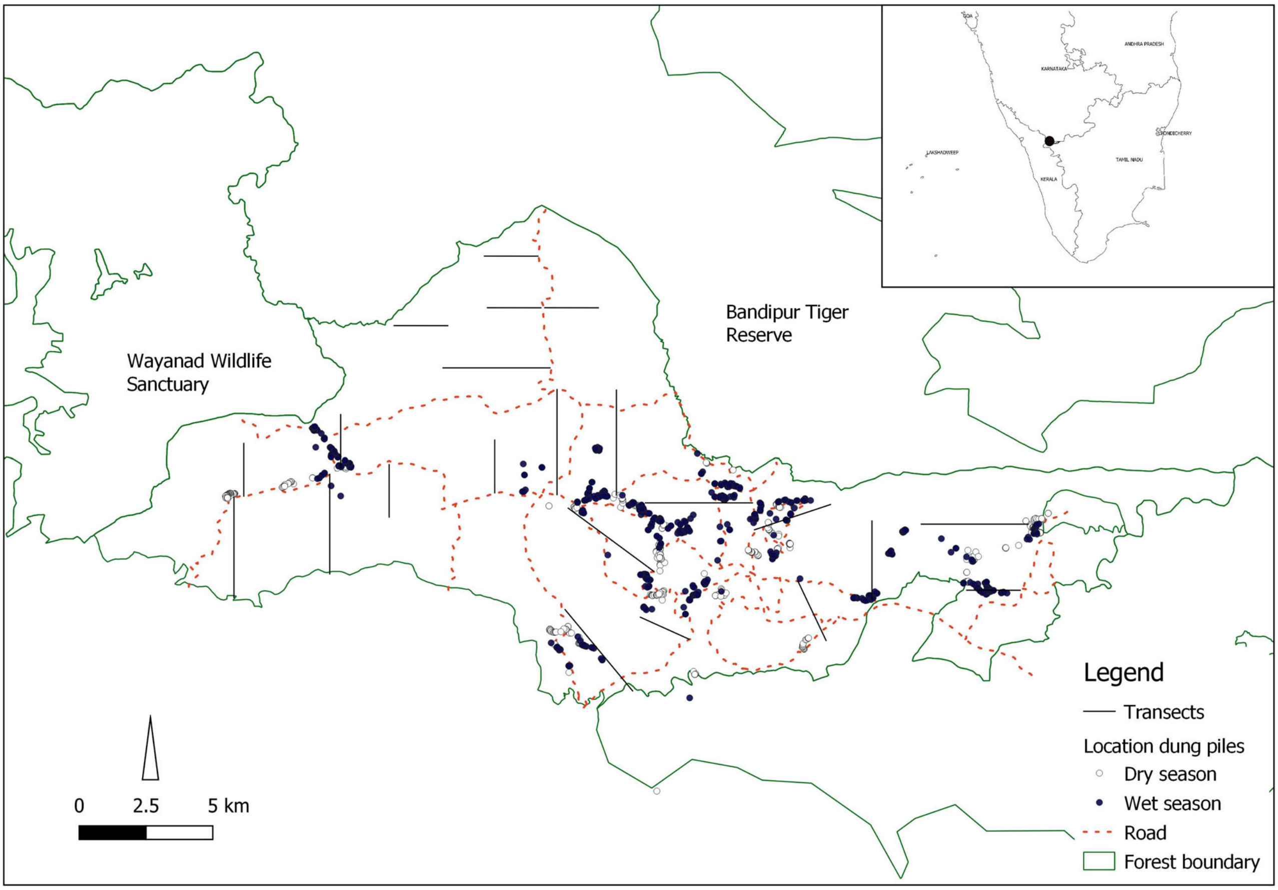

FIGURE 1 Map of the study area location showing transect lines and dung piles marked in theMudumalai Tiger Reserve

way to measure age composition, dung surveys also provide population demography based on dung size measurements (Jachmann & Bell, 1984; Morrison et al., 2005; Reilly, 2002). We estimated the growth curve based on dung measurements of Asian elephants in south India. Further, a limited number of studies on the reliability of the dung count method were compared with other methods (Barnes, 2001). The results of the study can be applied to other large herbivores and other mammal species with a longer life span.

We tested four hypotheses, that is, the age-specific defecation rate, dung decay rate, detection probability and age structure of the elephant population derived from dung count. We modelled the relationship between age and defecation rate to predict defecation rates. The estimated age-specific density can be used to understand the population age structure. We hypothesize that there is a higher probability of detecting the dung piles of adult animals than the smaller piles of juvenile animals. In an experiment, we evaluated dung piles that were available in the field and that were not detected during the transect walk.

2 | MATERIALS AND METHODS

2.1 | Study area

Line transect surveys, age–sex composition and elephant dung decay rates were estimated in the Mudumalai Tiger Reserve. The defecation rate of elephants was estimated in semi-wild animals in elephant camps at Mudumalai in the Nilgiris district of Tamil Nadu state, India (11° 32′ and 11° 42′ N and 76° 20′ and 76° 45′ E). The tiger reserve extends over an area of 321 km^2 and forms a part of the Nilgiri Biosphere Reserve (Figure 1). The reserve is located in the Western Ghats, which is one of the 35 biodiversity hotspots of the world (Myers et al., 2000). The altitude in the study area varies from 485 to 1226 m above mean sea level, with a general elevation of about 900 to 1000 m. There are densely populated human settlements on its south-eastern boundary and some smaller settlements inside the reserve. The study area has three major forest types, namely tropical moist deciduous , tropical dry deciduous and southern tropical thorn forest (Champion & Seth, 1968). Rainfall varies from 600 mm in the eastern part to 2000 mm in the western part of the reserve.

2.2 | Defecation rate

The defecation rate of semi-wild Asian elephants was gathered for different age–sex classes at the forest elephant camp at Mudumalai. A total of 14 elephants in the dry season (December 2001–March 2002) and 17 elephants in the wet season (June–October 2007) of different age–sex classes were observed for 42 days and 51 days, respectively (Table 1). Each elephant was followed for three consecutive days to quantify the defecation rate, thus resulting in a sampling effort of

TABLE 1 Defecation rate (per day) of the Asian elephant in different seasons and across age-sex classes (dry season $n = 14$; wet season $n = 17$)

	Wet ($n = 612$ h)		Dry ($n = 504$ h)		
Age class	Mean ± SE (number of elephants observed[a])	95% CI of mean	Mean ± SE (number of elephants observed[a])	95% CI of mean	ANOVA
Adults	13.68 ± 0.73 (10)	12.23, 15.14	16.04 ± 0.63 (12)	14.79, 17.29	$F_{(1,92)} = 9.71$; $p < 0.05$
Adult male	15.68 ± 0.77 (7)	14.15, 17.21	17.83 ± 0.70 (6)	16.43, 19.22	
Adult female	9.89 ± 1.06 (3)	7.78, 12.00	13.48 ± 0.84 (6)	11.81, 15.15	
Sub-adults	10.56 ± 0.90 (4)	8.78, 12.35	–	–	
Juveniles	–		10.41 ± 1.12 (2)	8.19, 12.64	
Calf	2.0 ± 0.01 (3)	–	–	–	
Overall	11.97 ± 0.68 (17)	10.59, 13.35	14.99 ± 0.68 (14)	13.60, 16.36	
ANOVA	$F_{(3,90)} = 15.6$; $p < 0.001$				

Abbreviations: ANOVA, analysis of variance; CI, confidence interval; SE, standard error.
[a]Each elephant with three replicates (3 days of observation).

504 and 612 h of observation in the dry and wet seasons, respectively. Elephants were observed by the focal animal sampling method (Altmann, 1974) during the daytime for 12 h, from 6:00 h to 18:00 h. All the activities were recorded with 10 min of observation and a 5-min interval. However, defecation occurring in the observer's interval time was noted, but other activities were not recorded. To determine the defecation rate, the interval between two defecations was averaged, that is, If a total of 10 defecations were observed over 10 h (observation duration from the first defecation to the last defecation), then an average of nine intervals (n − 1) was calculated (10 h/9 intervals = average defecation interval, x). The daily defecation rate was calculated by $24/x$. Thus, the defecation rates were calculated based on daytime (12 h) observations.

The number of nighttime defecations was determined in the wet season alone by counting the number of dung piles at the site where the elephant was tethered (where cut fodder was provided). Free-ranging semi-wild elephants, which are released into forest areas after evening food supplements, with their forelegs shackled together with a long trailing chain to track them the next morning. The nighttime defecations of these elephants were determined by counting the number of dung piles encountered along the trail of the chain, indicating the exact path of the animal. The nighttime defecation data were used to test the difference between day and night defecation alone for selected animals (adult male: seven elephants; adult female: three; sub-adult: four). Elephants were given food supplements in the morning and evening (cooked finger millet, horse gram and coconut) and then released into the forest for free grazing. Hence, the behaviour (foraging time) and the major diet of these elephants were similar to those of wild elephants (Ashokkumar, 2002; Vanitha et al., 2008). These elephants ranged over 2–4 km^2 around the elephant camp and foraged on natural vegetation.

The differences in the mean defecation rate across age–sex classes and seasons were tested by a two-way analysis of variance. The differences between day and night defecation were tested for selected elephants using a paired t-test using base R software. The defection rate was regressed with age and modelled using an exponential model (Equation 1) for both sexes together and separately using the 'lm' function in base R software.

$$y = \exp\left(a + (b/x)\right), \tag{1}$$

where y is the defecation rate/day, a is a constant, b is a regression coefficient, and x id the age of elephant. The validity of the model was tested using a paired t-test of observed and predicted defecation rates for a specific age class in base R software.

2.3 | Relationship between dung bolus size and age

Measurements of dung bolus circumference were collected while observing elephants for estimation of defecation rate in the above-mentioned methods. A total of 17 male and 10 female elephant dung boli measurements were used. At each defecation, the largest intact bolus circumference was measured. The mean dung boli diameter is calculated from the dung bolus circumference with the equation dung boli diameter (d) = circumference (c)/π.

The Von Bertalanffy growth equation (VBGM) is useful for fitting vertebrate growth data (Ebert, 1999) and has been used in modelling elephant growth (Lee & Moss, 1995; Morrison et al., 2005; Reilly, 2002). The VBGM was used to construct the growth models and is defined by the growth parameters L, K and t_0, and the length measurement L (Von Bertalanffy, 1938; Equation 2) in this study was the mean dung boli diameter to interpolate the growth of elephant.

$$L_t = L_\infty (1 - \exp)^{-k(t - t_0)}. \tag{2}$$

This equation is characteristically asymptotic, where L is the theoretical maximum size of the length measurement (dung bolus diameter), K is the coefficient of catabolism (growth decay constant) and t_0 is the theoretical age at 0 (Ebert, 1999). The interpretation of growth parameters concerning elephant growth is discussed in Lee and Moss (1995), Reilly (2002) and Morrison et al. (2005). The Von Bertalanffy growth was fitted using packages 'FSA', 'FSAdata' and 'nlstools' in R software (R Development Core Team, 2011). The predicted values of dung boli diameter between males and females were compared using paired *t*-tests in base R software.

2.4 | Age structure

Dung size has been correlated with the size (height) of elephants and, consequently, to estimate age class (Morrions et al., 2005; Reilly, 2002). To determine the age of the dung bolus diameter (calculated from the circumference measured at the large end of dung bolus), the growth parameters were rearranged in the VBGE equation (Equation 3) to predict the mean age (t) from the dung bolus diameter (L) measured in the dung transect.

$$t = -\left(\left(t_0 - (1/-k)\right) * (\ln(1 - L/L_\infty)\right). \tag{3}$$

As the asymptotic size is reached, the sensitivity of the growth model to changes in diameter increases greatly, such that a small increase in the diameter could indicate a large increase in age. Therefore, dung bolus diameters greater than 15 cm, which was an asymptotic size, were grouped together and denoted as 20+ years.

2.5 | Detection of dung piles

The detection of various age class and size classes of dung at a different perpendicular distance was measured using an experimental two belt transect in tropical dry deciduous forest with a length of 2 km and a width of 25 m on either side of the transect. The age class of dung piles was determined based on dung (intact bolus circumference measured at the large end) measurements. Initially, dung piles visible from the transect were counted and marked with calcium carbonate powder to identify them as detected dung piles.

After completion of the transect count, the dung piles that were present within a width of 25 m on either side of transects that were not detected from the transect were recorded as missed dung piles. A 100-m rope was kept in the middle of the transect, and then the entire area was searched by four observers walking at a 5-m interval on one side of the transect. All missed dung piles in the transect were recorded with details of perpendicular distance, the extent of dung spread, that is length and width of dung spread, the presence of boli and dung bolus circumference were measured. Then the other side of the transect was surveyed using the same method. The proportion of dung piles detected at different perpendicular distances was calculated by dividing the number of dung piles detected by the sum of the number of detected and non-detected dung piles at a particular distance.

The dung pile status, that is observed or missed, was coded as 1 and 0, respectively. Differences in detection were tested against independent predictors, that is, perpendicular distance, age class (adult, subadult, juvenile and calf) of dung were tested using binary logistic regression using the 'glm' function in R software.

2.6 | Dung survival rate

The elephant herds were located and tracked, and fresh dung piles (less than 6 h old) were marked in all three habitat types. Every month, an average of 125 ± 77 fresh dung piles/month was marked using numbered bamboo stakes from January 2007 to February 2008. Variables such as geographic location, age class estimated based on dung circumference, grass composition, canopy cover and total length and width of dung spread were noted. Every month, dung piles were marked in different habitats and revisited every 15 days to assess the status of dung piles (Figure 1). To estimate the survival rate of dung piles, based on a retrospective method dung piles were examined one day before the survey during dry and wet seasons (Hedges & Lawson, 2006; Laing et al., 2003).

A total of 1551 dung piles were marked and monitored over 13 months, but for decay rate analysis, only the relevant months (6 months prior to the survey) before the dung density transects were run were used. The dung decay rate was estimated using the retrospective method (Laing et al., 2003). The dry season survey was started on 15 March 2008, and the wet season was started on 20 July 2007. Dung piles that had decayed were denoted as 0, while those that had not decayed were denoted as 1. The dung survival rate was estimated using logistic regression to find differences in the decay rate across seasons and age classes of the elephant. Models based on the maximum likelihood estimation of parameters were analysed with the 'glm' function family of the statistical package in base R using a modified code of the CITES MIKE program (Hedges & Lawson, 2006; R Development Core Team, 2011).

Variables in the analysis are the predictor variable age (day) and response variable state of dung piles, that is presence/absence. The mean time to decay (decay) was computed from the dung age t using Equation (4) (Laing et al., 2003):

$$\text{Decay} = \int_0^\infty \frac{-\beta_1 t\,[1 + \exp(-\beta_0)]\exp[-(\beta_0 + \beta_1 t)]}{[1 + \exp\{-(\beta_0 + \beta_1 t)\}]^2}\,dt, \tag{4}$$

where the intercept β_0 and the slope β_1 of age t were obtained from logistic regression (Laing et al., 2003). Age-specific and seasonal differences in the mean survival rates were tested using the Student t-test.

2.7 | Age-specific elephant density

The dung density was determined using the indirect dung count method. A total of 24 transects of 2–4 km, resulting in a total distance of 125 km (56.5 km in the dry season and 68.5 km in the wet season), were walked (Figure 1). Transects were placed randomly in the study area to get adequate spatial coverage and proportional representation of three habitat types, similar to an earlier study (Baskaran et al., 2010). Dung piles that were visible from the transect were counted, and the perpendicular distance was measured using a measuring tape. The dungs were categorized into the 'S system' based on the stage of decay of dung piles (S1, all boli intact; S2, one or more boli intact; S3, no boli intact with coherent fragments remaining; S4, only traces of dung fragments remaining) of the Mike dung pile classification system (Hedges & Lawson, 2006). All the dung piles encountered (S1 to S3) in the transects used to estimate dung density were measured. The largest circumference of an intact bolus in a dung pile was measured. If all the dung boli were not intact, the corresponding age class was denoted as unknown. The survey was completed within a month (July 2007 wet and March 2008 dry).

Distance 7.2 software was used to estimate overall and age-specific elephant densities (Buckland et al., 2001; Thomas et al., 2010). The age of the elephant was determined based on the dung bolus diameter encountered in the transect using Equation (3). The number of detections of dung piles across specific ages was less, and hence they were grouped into 1–3, 4–7, 8–11, 12–15, 16–19, and 20+ age categories to estimate densities. The defecation rate was estimated using prediction equation (1), and the mean decay rates for specific age classes were entered separately as multipliers to obtain density for the specific age class. We first carried out an exploratory analysis as described by Buckland et al (2001). The program models the detection function, and a priori models such as half-normal (with cosine adjustment) and hazard rate (with cosine adjustment) were used. The Akaike Information Criterion, visual examination of model fit and goodness-of-fit tests were used to select the best model fit. Using the model thus selected, estimates of elephant density were derived using Equation (5).

Elephant density (individuals km^2) total and age-specific was calculated as shown in Equation (5) (Wing & Buss, 1970)

$$D = N_{\mathrm{dung}} / D_{\mathrm{md}} / P, \tag{5}$$

where D is the estimated age-specific elephant density (individuals km^2), N_{dung} is the estimated age-specific dung density (dung samples km^2), D_{md} is the estimated age-specific mean time to decay (/day), and P is the estimated defecation rate for an age class (dung samples/individual and day).

3 | RESULTS

3.1 | Defecation rate

The overall defecation rate for 31 elephants observed over 3 days per elephant was 13.51 ± 0.51 (n = 94) per day (24 h). The mean defecation rates for adult males and females (irrespective of the season) were 16.85 ± 0.55 and 12.10 ± 0.80, respectively. The defecation rate varied significantly between adult males and females ($F_{1,66} = 25.43$, $p < 0.001$). The defecation rates of sub-adults (both sexes combined), juveniles (males) and calves were 10.56 ± 0.90, 10.41 ± 0.87 and 2 ± 1.94, respectively. Thus, the defecation rate varied significantly among different age classes ($F_{3,90} = 15.57$, $p < 0.001$). The defecation rate varied among different seasons with a higher defecation rate during the dry season than during the wet season ($F_{1,92} = 9.713$, $p < 0.05$). The two-way interaction between the defecation rate of different age-sex classes and seasons was also significantly different ($F_{5,89} = 232.51$, $p < 0.001$) with a higher defecation rate observed during the dry season for both males and females (Table 1).

Observation of selected animals revealed that the defecation rate for adult male elephants was significantly lower at night (5.6 ± 0.26) than during the day (7.6 ± 0.36; $t_{(20)} = -5.61$; $p < 0.001$). Female elephants also had significantly less defecation at night (4.1 ± 0.33) than during the day (5.0 ± 0.01; $t_{(8)} = -8.0$; $p < 0.001$). However, the defecation rate for sub-adults was constant across day and night with 5.8 ± 0.25 and 5.3 ± 0.22, respectively ($t_{(11)} = -1.603$; $p > 0.05$).

The relationship between the age of an elephant and the defecation rate was related to the exponential model. The defecation rate increased significantly with the age of the animal (Figure 2). The regression equation model for both sexes was $y = \exp\,(2.71 + (-2.01/\mathrm{age})$ with $R^2 = 0.55$, and it was highly significant ($F_{(1,93)} = 115.9$; $p < 0.001$). The prediction equation for a male elephant was $y = \exp\,(2.87 + (-3.05/\mathrm{age}))$; $R^2 = 0.29$; $F_{(1,60)} = 24.99$; $p < 0.001$), and for females it was $y = \exp(2.54 + (-1.81/\mathrm{age}))$; $R^2 = 0.75$; $F_{(1,31)} = 91.36$; $p < 0.001$). The age-specific comparison of observed and predicted defecation rates was similar ($t_{(24)} = -1.12$; $p > 0.05$).

3.2 | Relationship between dung bolus size and age

The VBGE was fitted for age and dung bolus diameter for each sex separately (Figure 3). The growth of elephants and increase in anal size resulted in the increase in dung bolus diameter rapidly from 0 to 15 years for both sexes. A female elephant dung bolus reaches an asymptote early at the age of 25 years, and it is 30 years for males. The derived growth parameters for the dung boli diameter for both sexes and their confidence interval of the VBGE are Linf = 14.89 ± 0.39 (14.15, 15.64); $t_0 = -3.27 \pm 1.88$ (−7.14, 0.60); $K = 0.12 \pm 0.029$ (0.06, 0.19). The male elephant growth parameters are Linf = 15.7 ± 0.32 (15.04, 16.41); $t_0 = -2.62 \pm 1.99$ (−6.82, 1.59); $K = 0.12 \pm 0.03$ (0.06, 0.17). The female elephant growth parameters are Linf = 13.6 ± 0.71 (11.89, 15.4); $t_0 = -5.7 \pm 5.24$ (−18.54, 7.13); $K = 0.10 \pm 0.06$ (−0.05, 0.25). A comparison of predicted dung boli diameter at a specific age class showed that female elephant dung bolus diameter was significantly lower than the male ($t_{(79)} = 23.90$; $p < 0.001$).

3.3 | Age structure predicted from dung diameter

The dung bolus encountered in the transect was measured, and age was predicted using the VBGE Equation (3). Most of the dung piles recorded were in the decay stage of S2 and S3 with one or two dung boli were available to measure, so we were able to measure the dung circumference. A total of 1082 (98%) and 1029 (73.3%) dung boli were measured to predict the age class in the dry and wet seasons, respectively. The age structure revealed 60% and 49% of the above 20-year age class during the dry and wet seasons, respectively (Figure 4). In total sub-adults (6–15 years), dung boli were 29.4% and 41.5% in the dry and wet seasons, respectively. In younger age classes, juveniles constituted < 5% of the

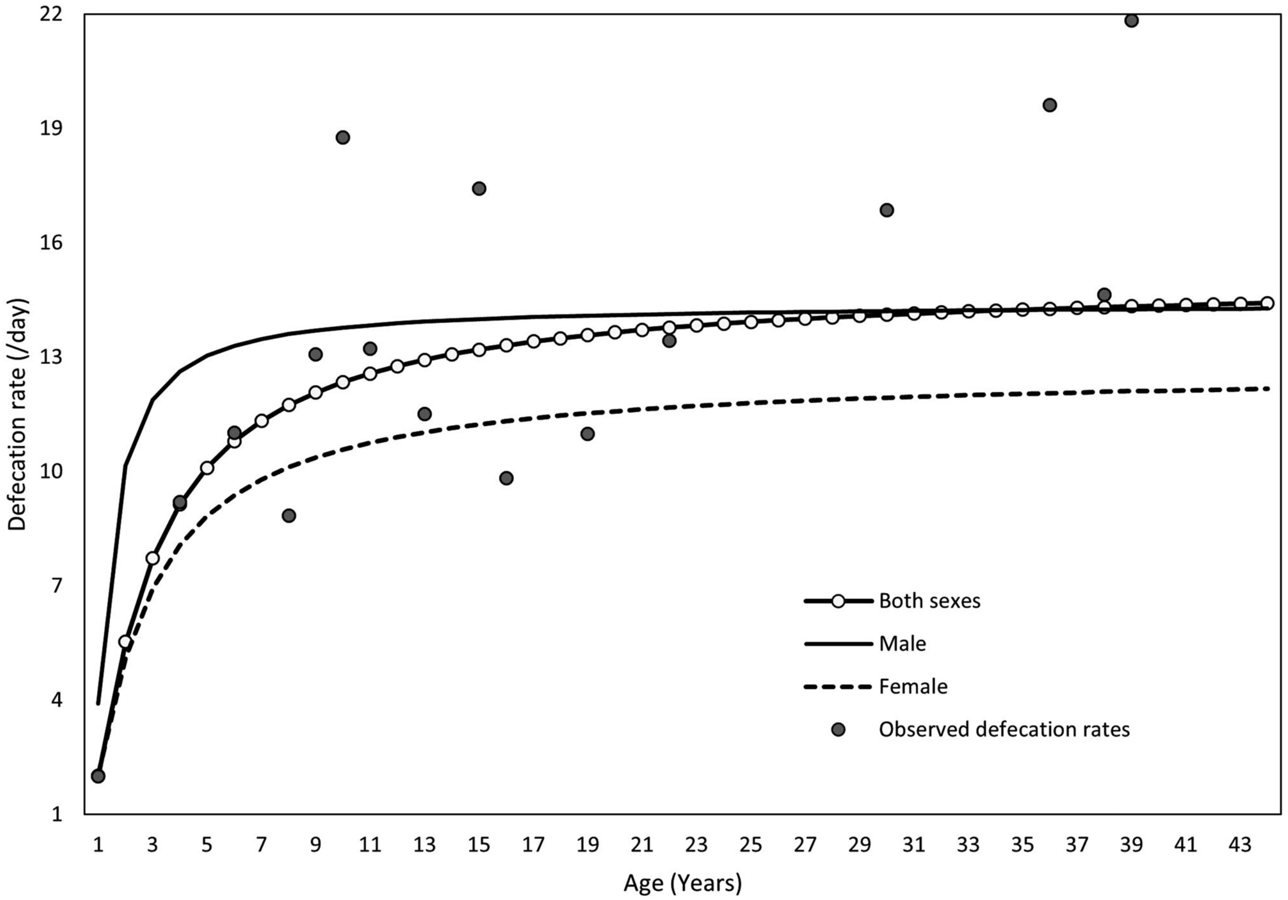

FIGURE 2 The modelled defecation rate shows the relationship between the age and sex of the elephants and defecation rates

total and calves constituted ~1%. A much smaller number of dung boli were recorded in the 14–19 year age category.

3.4 | Detection of different age classes of dung

The detection of different age class dung piles at different perpendicular distances from the transect varied. Within the visible range of a perpendicular distance of 10 m, the probability of detection of adults and sub-adults was greater than 0.91. However, it was only 0.88 and 0.58 for juvenile and calf, respectively (Supporting Information Figure 1a). At the furthest distance from the transect line (beyond 10 m), the detection of adult, sub-adult, juvenile and calf was 0.74, 0.43, 0.33 and 0.17, respectively. Hence, juvenile and calf dung piles had a lower probability of detection within the observer's visible distance in the transect, and it was further lowered as the distance increased from the transect.

3.5 | Dung survival rates

The mean survival rate of dung piles ranged from 22 to 177 days, and it was higher in the wet season (133.69 days) than in the dry season (117.81 days). In the wet season, dung survival rates increased with the age of elephants, with calf dung piles decaying faster (89 days) and adult dung piles surviving longer (141 days; $t_{(19)} = 3.03$; $p < 0.05$; Figure 5). However, the dung piles of 4- to 6-year-old elephants survived longer (177 days) in the wet season. Dung survival days are around the mean value of 118 days in the dry season across all ages. Thus, the wet season decay rate alone differed across the ages.

3.6 | Age-specific elephant density

The age-specific estimate of dung density revealed a higher density of elephants older than 20 year, followed by the 12–15 year age categories (Table 2). For instance, the density estimates for the 1–3 age category, dung numbers encountered were 19 and 25, dividing the values by appropriate defecation and decay rates results in elephant numbers of 25 and 71 in the wet and dry seasons, respectively. Thus, the use of age-specific defecation and decay rates corrected the bias in the estimate. Similarly, the adult dung piles (above 20 years) encountered were 504 and might be the result of higher defecation, the use of age-specific defecation has lowered the estimated elephant population (202) in the wet season. Similar age-specific changes in elephant density estimated from dung numbers can be seen in the dry season. The estimated ele-

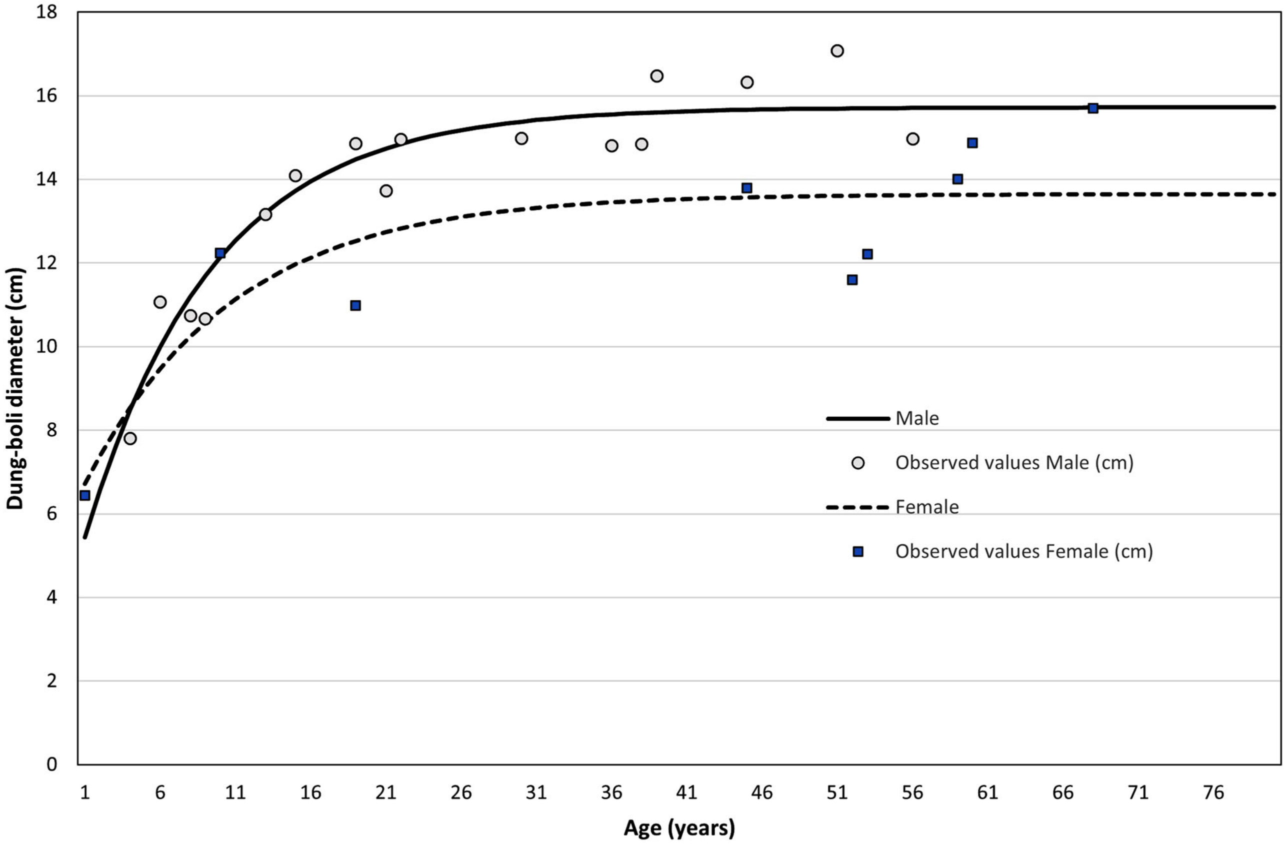

FIGURE 3 Relationship between age and dung bolus diameter based on the Von Bertalanffy growth model based on elephants of known age at the Mudumalai Tiger Reserve

TABLE 2 Age-specific estimate of elephant density and estimated elephant population for the study area

Seasons	Age category (years)	*n*	ESW (m)	Density (km^2)	95% of CI of mean Lower	95% of CI of mean Upper	CV (%)	Estimated population
Wet (68.5 km)	1–3	19	1.8	0.08 ± 0.07	0.02	0.35	86.00	25
	4–7	437	2.85	0.14 ± 0.09	0.05	0.42	58.74	45
	8–11	170	3.42	0.16 ± 0.07	0.07	0.38	46.96	51
	12–15	161	2.47	0.31 ± 0.10	0.17	0.56	30.95	100
	16–19	37	2.84	0.05 ± 0.02	0.02	0.11	42.00	17
	20+	504	2.16	0.63 ± 0.15	0.39	1.01	24.30	202
	Total	1402	2.19	2.20 ± 0.44	1.48	3.27	20.20	706
Dry (56.5 km)	1–3	25	1.96	0.22 ± 0.11	0.08	0.59	52	71
	4–7	110	4.06	0.46 ± 0.18	0.21	0.99	39.8	148
	8–11	113	3.01	0.24 ± 0.11	0.09	0.57	46.4	77
	12–15	129	5.8	0.12 ± 0.04	0.06	0.23	30	39
	16–19	52	5.5	0.044 ± 0.02	0.02	0.09	42	14
	20+	633	4.9	0.63 ± 0.18	0.36	1.12	27.8	202
	Total	1456	3.65	2.02 ± 0.33	1.45	2.81	16.2	648

Abbreviations: ESW, estimated strip width (m); CI, confidence interval; CV, coefficient of variation.

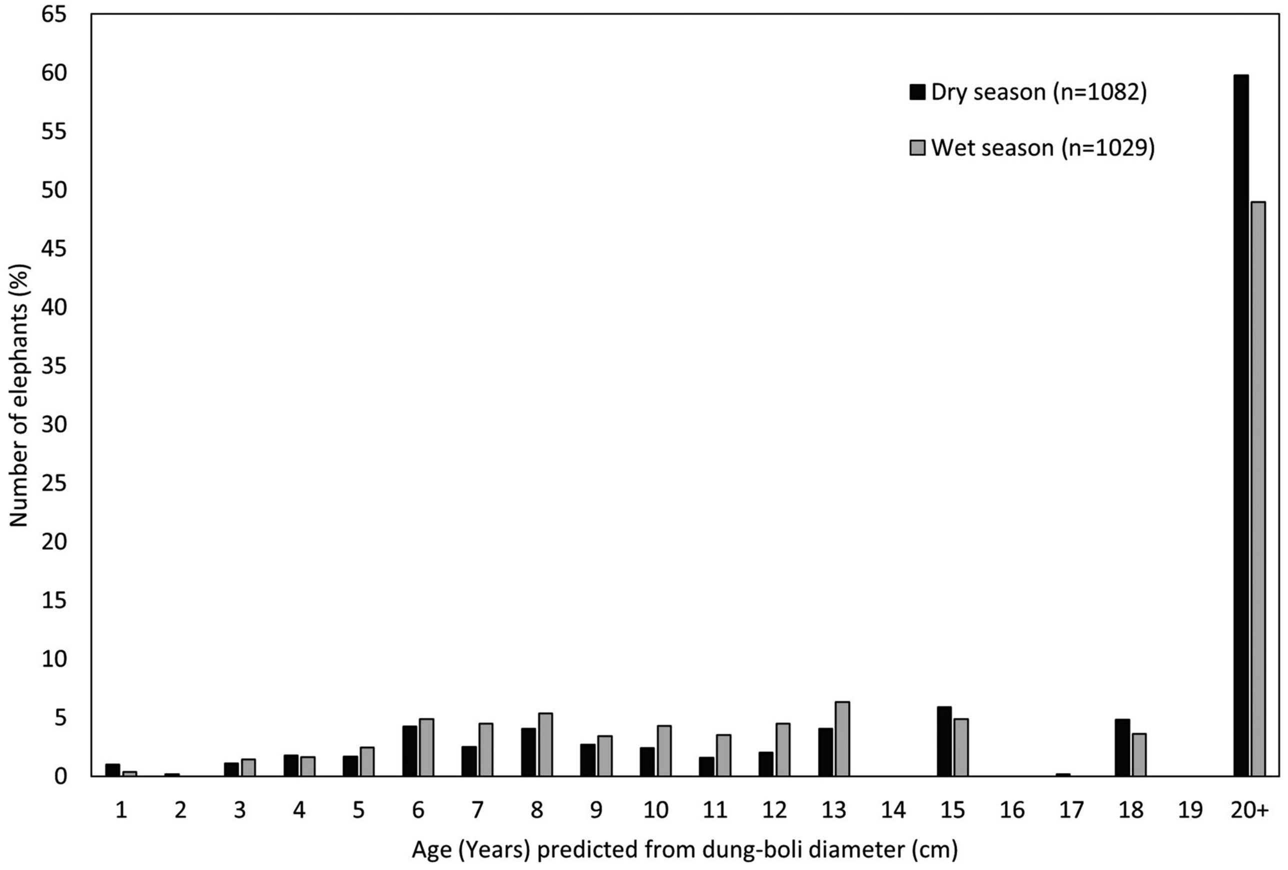

FIGURE 4 Age structure of the elephant population at the Mudumalai Tiger Reserve predicted from dung bolus diameter measured

phant density was marginally higher in the wet season (2.20) than in the dry season (2.02). The estimated densities of the younger age classes (1–3 years) and 16–19 year age categories were low in the population (Figure 6).

The comparison of age structure based on direct dung measurements and age-specific estimated elephant population revealed that the percentage of the above 20 years age class comprised 36–46%, which is lower than the direct dung measurement values of 49% and 60% in the dry and wet seasons, respectively (Figure 4). The percentage composition of younger age categories was considerably greater than that of the direct dung-based assessment. Thus, it is essential to correct the age structure data based on dung measurements.

4 | DISCUSSION

The age-specific differences in Asian elephant defecation rate, demography based on dung bolus diameter, detection of dung and decay rate were evaluated. Defecation rates increased with the age of elephants, and the defecation rate can be predicted based on the model suggested. The age of elephants can be estimated using dung bolus diameter and can be used to predict age structure in the indirect count method. Age structure derived from dung measurements underestimates the younger classes and has limitations in determining the age above 20 years. Dung detection experiments revealed that younger age class dung piles had lower detection near the observer. The dung survival rate increased with the age of elephants only in the wet season. Age-specific estimates of density had lower estimates for young elephants.

Adult elephants defecate more frequently than younger elephants, with significantly higher defecation rates observed in the dry season. It varied across the day, with more frequent defecation during the day than at night. The reported defecation rates in this study are slightly lower than those reported for the wet season (14.6/day) by Dawson (1990) in the study area. Seasonal and intra seasonal variations in the defecation rates were reported in earlier studies on Asian elephants (Dawson, 1990; Reilly, 2002). Similarly in Africa, a study by Theuerkauf and Ellenberg (2000) showed some differences between wet (16.6/day) and dry (18.1/day) season defecation rates. Seasonal variation in defecation might be due to variations in the protein, fiber, and moisture content of food (Barnes, 1982; Dawson, 1990; Guy, 1975). Tchamba (1992) reported a defecation rate of 19.77/day (combined wet and dry seasons) for elephants in Cameroon, and although this was a wet evergreen forest habitat such as the study area of Theuerkauf and Ellenberg (2000) (in Ivory Coast) the rates of defecation differed. Therefore, different sites are likely to have different rates based on the local conditions and diet of the elephant. The generalization of elephant defecation rate based on the rainfall model (Theuerkauf & Gula, 2010) has

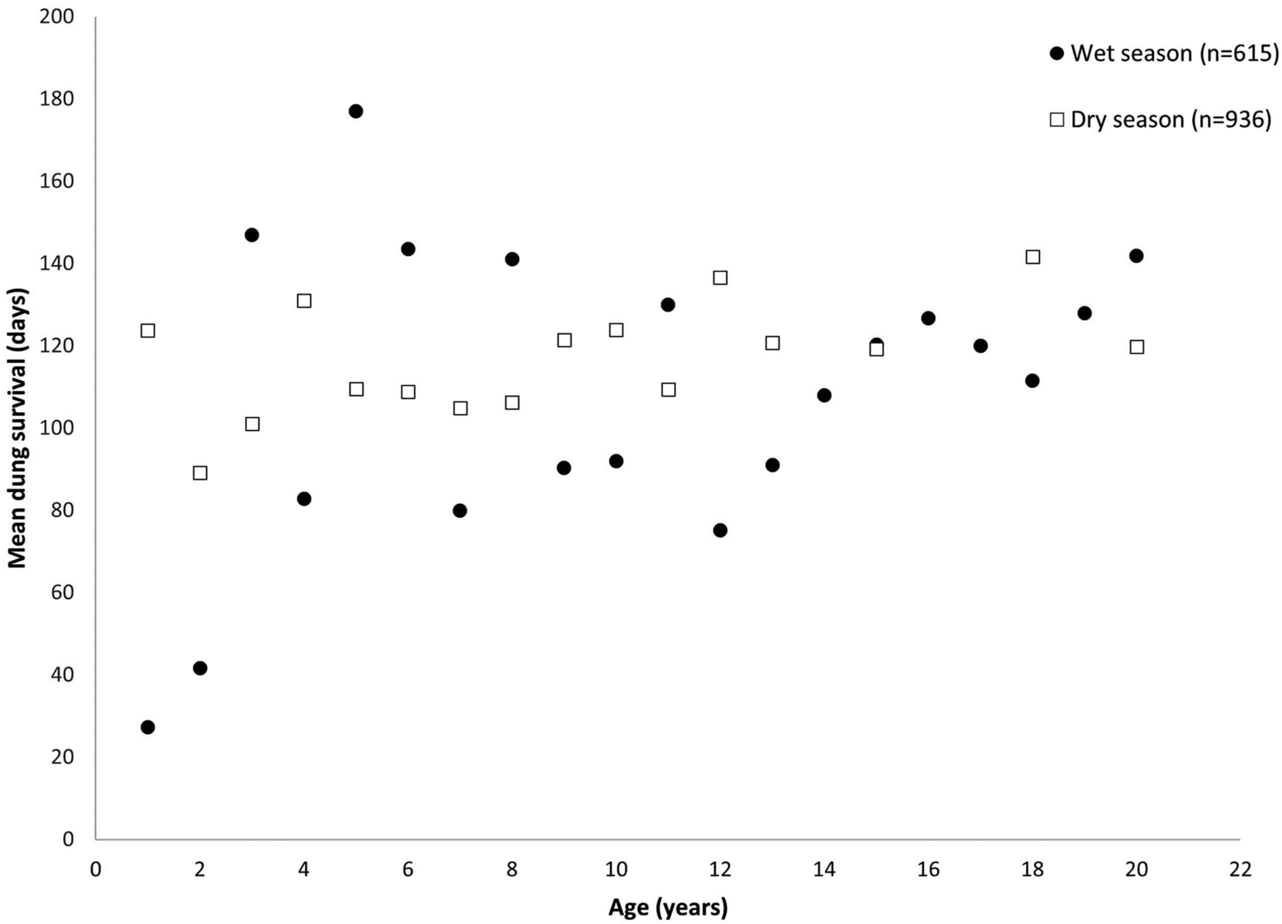

FIGURE 5 Mean survival rate of dung piles (days) of elephants estimated from logistic regression in different seasons and across age

to be dealt with caution since there is variation in the defecation rates within a particular season.

The present study brings into focus another aspect that has not been reported earlier, namely differences in defecation rates between different age–sex classes and across the day. The variation in defecation across days necessitates a 24-h observation period. For an elephant population with a higher composition of adults and sub-adults, the use of the adult defecation rate would correctly estimate the density. Adults and sub-adults have similar defecation rates. In a population with many younger animals, the use of adult defecation rates could potentially underestimate the density. Hence, it is essential to assess the age structure based on dung bolus diameter and correct the bias of defecation in the density estimate.

The defecation rate significantly increased with the age of the elephant. The defecation rate prediction model can be used to predict the defecation rate for any age–sex class. Body size, sexual dimorphism and the quantity of food consumed vary across the sexes and age classes, which results in differences in defecation rates. Further, a higher defecation rate enables us to encounter a greater number of dung piles available to count, thus reducing variation in the samples and improving the model fit between perpendicular distance and dung detection. Thus, the precision of the elephant population estimates using dung count is higher.

In this study, the growth models were used to predict the actual age of an animal from dung bolus diameter and to determine the population age structure. Dung bolus diameter measurement can be a reliable, easily measured, and non-invasive method to assess age or age structure, similar to forefoot measurements (Lee & Moss, 1995). The growth rates of dung were highest in the first 10 years of life, during lactation, and afterwards. Males' growth rates were initiated early, and dung boli diameter increased faster than females, producing a marked size difference between the sexes (Morrison et al., 2005). The growth patterns of dung piles were similar to those of other populations of Asian and African elephants (Lee & Moss, 1995; Reilly, 2002; Sukumar et al., 1988). The curve depicting growth in an average Asian elephant suggests that they continue to grow during adulthood. There are limitations in predicting ages for elephants with length measurements greater than the theoretical maximum (L_α) and as length approaches this asymptote at the age of 20 for females and 25 for males, the growth equations become increasingly sensitive to a small increase in size. As a result, the growth models are most sensitive to predicting ages up to 30 years. Further, Jachmann and Bell (1984) reported that there were regional variations in the growth curves of elephant populations. Thus, this growth curve can be used to estimate age class based on dung measurements in the southern Indian Asian elephant population.

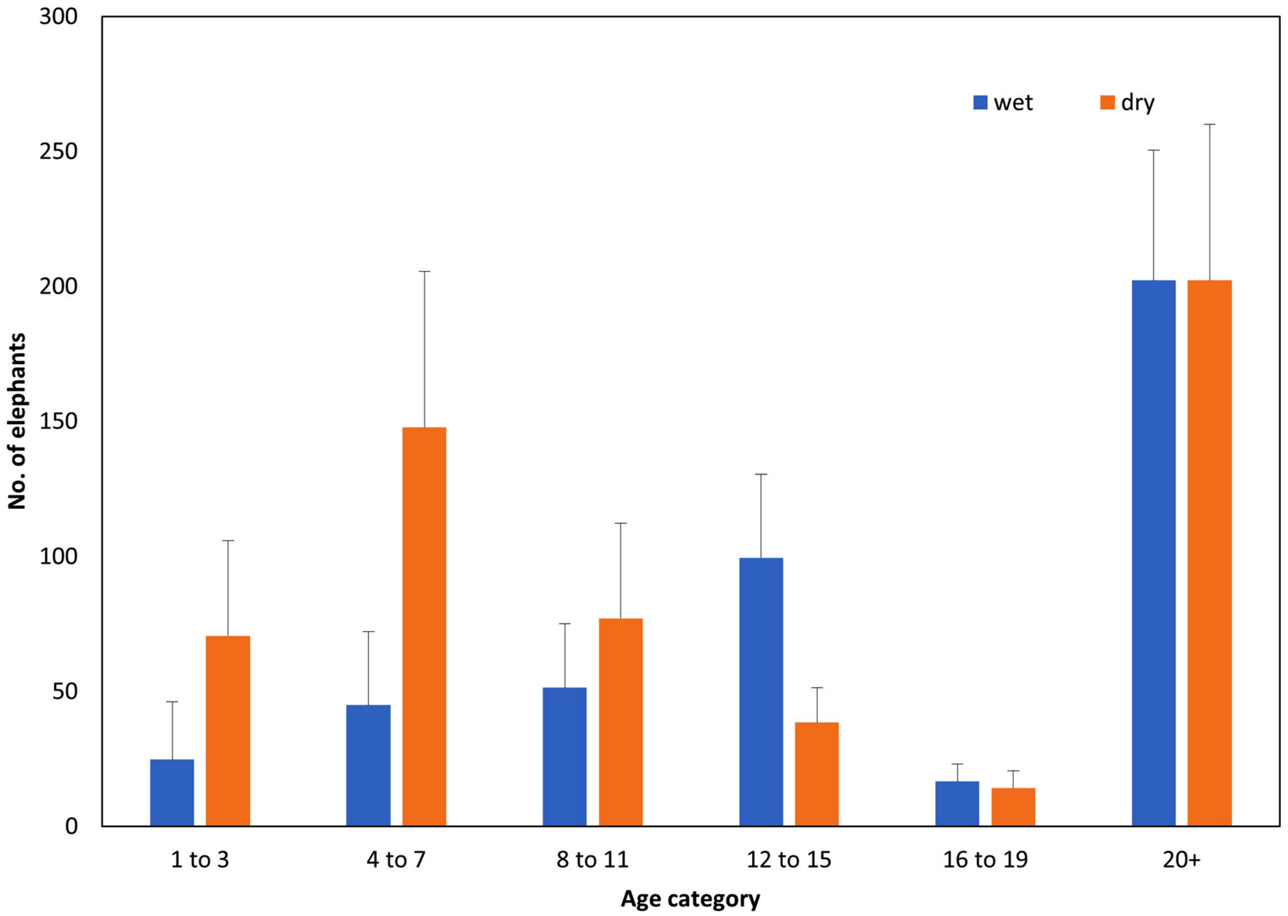

FIGURE 6 Age category wise elephant population (± SE) estimated using age-specific defection, dung decay rate and modelled detection function

Dung classification based on age class showed that juvenile and calf dung piles had a lower probability of detection within the observer's visible distance in the transect and this disparity in detection increased at the furthest distance. Hence, it is essential to classify the dung piles into age classes and estimate the densities for each age class. The size bias can be overcome by modelling detection by including dung size as a covariate (Buckland et al., 2001). This further supports the importance of age-specific density estimation. Detection of dung/species depends on factors such as the observer's experience of a similar survey, the size of the object/cluster and perpendicular distance. Observer efficiency in the detection of dung or counting animals can be increased by experience. Observer bias in detection can be determined by the two-observer sampling method (Nichols et al., 2000) and was tested in aerial counts of elephants in Africa (Schlossberg et al., 2016). Second, in the dung count, it is important to measure the dung bolus diameter, since there is variation in the detection probability of different age classes of dung.

The estimated days to decay were higher in the wet season (133.7 days) than in the dry (117.8 days) in the study area. Age-specific dung survival rates increased with the age of elephant within the wet season. Thus, dung pile persistence time was consistently higher in the dry season than in the wet season. Similarly, Oliver et al. (2009) reported that persistence times for dung piles were longer in the dry season than in the wet season in Africa. Seasonal and intraseasonal variation in dung decay has been reported in African elephants (Barnes et al., 2006; Nchanji & Plumptre, 2001; Oliver et al., 2009). Thus, the dung decay rate tends to vary depending on months, seasons and habitats. Earlier studies monitoring individual small and large boli of adult and sub-adult elephants reported non-significant decay rates (Oliver et al., 2009). In the current study, monitoring of entire dung piles of defecation in the forest revealed a significantly rapid decay rate for calves, followed by sub-adults and adults in the wet season. Thus, we report seasonal and age-specific differences in dung decay rates in tropical forests.

An important aspect of the decay experiment is how many samples were needed to estimate the decay rate. Hiby and Lovell (1991) recommended sample size of 100 dung piles to be monitored to determine the decay rate. The mean survival of dung piles was ~130 days, so cohorts of 50 dung piles marked per month for the 5 months prior to the survey would result in 250 dung samples. Hence, we recommend a sample size of 250 dungs of different age classes to estimate the decay rate.

Age structure derived from dung measurements overestimates adult elephants in the population (49–60%). Reilly (2002) reported a significantly lower proportion of calves in Sumatran elephants in the age structure estimated from dung measurements. Oliver et al. (2009)

reported a few newborns in the data extrapolated from the dung measurements of African elephants in the Maputo Elephant Reserve. Similarly, Hema et al. (2017) reported a lower percentage of calves in the age structure of African elephants derived from dung measurements, and they speculated on lower defecation, faster decay and low visibility of calf dung piles. Although the authors in the previous studies reported differences in the demography based on dung count, the exact reason for the difference could be due to these three factors. Direct dung measurements to estimate age structure overestimate adults in the population due to disparities in defecation. Hence, the derived dung count numbers need to be corrected based on age-specific defecation and decay rates.

In this study, we propose an age-specific density estimation of elephants. The direct count method estimated 48.5%, 16.6% and 14% of adults, sub-adults, and juveniles, respectively, in the population (Ashokkumar et al., 2010). In this study, the estimated age structure was similar among adults (31–33%), sub-adults (~18%) and juveniles (4–23%), whereas the estimates of calves were 8–15% lower in the dry and wet seasons, respectively. The density estimate could be lowered due to fewer dung samples (<30) to model the detection function. Hence, we underestimate the number of calves in the population.

The age-corrected estimates provide insight into the population's age structure. Age-specific population estimates indicate a lower number of 16 to 19-year-old age categories in the population. The lower abundance of this age category could be attributed to the impact of poaching in the past, 16 + 2 years (including gestation period) around the years 1989 to 1992 (calculated to the year of data collection 2007–2008). Earlier studies reported a highly skewed sex ratio of 1:29 in the study area due to selective poaching of males (Baskaran et al., 1995; Daniel et al., 1987). Further studies on the poaching of elephants in the Western Ghats reported that 336–388 elephants were poached in the previous 10 years (1974–1994) (Sukumar et al., 1998). Thus, the lower abundance of 16 to 19-year-old elephants could be attributed to the severe impact of poaching on the population.

The estimated elephant density was marginally higher in the wet season (2.20 ± 0.44) than in the dry season (2.02 ± 0.33). The differences in wet and dry seasons were due to local seasonal movements of elephants in the study area. Mudumalai Tiger Reserve is part of a larger elephant range that includes elephant reserves 7 and 8 and covers an area of over 1500 km^2. Elephants from Mudumalai have been shown to have large home ranges of over 600 km^2 (Baskaran et al., 1995), which is more than twice the size of the study area. Thus, the population estimate should be considered as an average number of elephants using the study area during the sampling period.

The present population estimate is higher than the earlier estimate of 1/km^2 (Daniel et al., 1987) and similar to the earlier estimate in 2000 by the direct count method (2.39 ± 0.72/km^2; Baskaran et al., 2010). The estimated density is lower than the direct count method conducted during the same period in the dry season (3.27 ± 1.39) in the study area (Daniel et al., 2008). Although there were differences in the estimates based on the two methods, the precision of the estimate from dung count is greater than that of the direct count method. The estimated elephant density and precision were similar to or higher than the estimate from the direct count method (2.24; 1.41–3.56) in the Nagarahole National Park in southern India (Jathanna et al., 2015). Direct sampling requires several temporal replications to increase the number of sightings (four to six replications per transect; Jathanna et al., 2015) and further invasion of exotic species in the forest areas hampers visibility in the transect, which could in turn influence the detection of animals and raise the possibility of an encounter with an elephant at a close distance. In the dung count method, the effort needed to estimate dung density is less. Further to estimate the decay rate forest-field staff can mark the dung piles prior to the survey, and the status of the dung piles can be enumerated at the time of the survey.

5 | CONCLUSIONS

In the present study, we propose an age-specific density estimation based on the dung count method. (1) The defecation rate significantly increased with the age of the elephant and varied between adult males and females, across age classes and seasons. The modelled defecation rate across ages can be tested in the other elephant population. (2) The age structure estimated from dung size revealed a lower per cent of younger animals. (3) An experimental study on dung detection revealed lower detection of younger age class dung piles. (4). The growth curve based on dung boli diameter can be used to estimate the age and age structure of the elephant populations. (5) The use of age-specific defecation rate, decay rate and modelling of detection of dung piles age-wise could predict the actual age structure of the population. (6) Dung-based age structure assessment has limitations in predicting age structure for young elephants and those above 20 years. Further combinations of direct and indirect methods can be used to estimate elephant populations and age compositions. The comparison of dung count and faecal DNA-based capture-recapture estimation (Gray et al., 2014) can be tested in elephant ranges. DNA-based methods provide further insight into population structure and genetic relatedness.

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CONFLICT OF INTEREST

We do not have any conflicts of interest to disclose.

AUTHOR CONTRIBUTIONS

MA was Involved in data collection, developed theory, performed computation and prepared manuscript. SC and SK assisted in the field sample collection and preparation of the manuscript. SS and AAD supervised the work and reviewed the manuscript. All authors discussed the results and approved to the final manuscript

DATA AVAILABILITY STATEMENT

Raw data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.1vhhmgqvs (Ashokkumar, 2022)

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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