

ARTICLE

Methods, Tools, and Technologies

Improving population analysis using indirect count data: A case study of chimpanzees and elephants

Samuel Ayebare^{1,2,3}  | Neil A. Gilbert^{1,2}  | Andrew J. Plumptre^{4,5}  |
Simon Nampindo³ | Elise F. Zipkin^{1,2} 

¹Department of Integrative Biology,
Michigan State University, East Lansing,
Michigan, USA

²Ecology, Evolution, and Behavior
Program, Michigan State University, East
Lansing, Michigan, USA

³Wildlife Conservation Society (WCS),
Uganda Program, Kampala, Uganda

⁴KBA Secretariat, c/o BirdLife
International, Cambridge, UK

⁵Conservation Science Group,
Department of Zoology, Cambridge
University, Cambridge, UK

Correspondence

Samuel Ayebare
Email: ayebares@msu.edu

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Abstract

Estimating spatiotemporal patterns of population density is a primary objective of wildlife monitoring programs. However, estimating density is challenging for species that are elusive and/or occur in habitats with limited visibility. In such situations, indirect measures (e.g., nests, dung) can serve as proxies for counts of individuals. Scientists have developed approaches to estimate population density using these “indirect count” data, although current methods do not adequately account for variation in sign production and spatial patterns of animal density. In this study, we describe a modified hierarchical distance sampling model that maximizes the information content of indirect count data using Bayesian inference. We apply our model to assess the status of chimpanzee and elephant populations using counts of nests and dung, respectively, which were collected along transects in 2007 and 2021 in western Uganda. Compared with conventional methods, our modeling framework produced more precise estimates of covariate effects on expected animal density by accounting for both long-term and recent variations in animal abundance and enabled the estimation of the number of days that animal signs remained visible. We estimated a 0.98 probability that chimpanzee density in the region had declined by at least 10% and a 0.99 probability that elephant density had increased by 50% from 2007 to 2021. We recommend applying our modified hierarchical distance sampling model in the analysis of indirect count data to account for spatial variation in animal density, assess population change between survey periods, estimate the decay rate of animal signs, and obtain more precise density estimates than achievable with traditional methods.

KEYWORDS

chimpanzees, elephants, indirect counts, marked sign count, population change, spatial abundance patterns

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INTRODUCTION

Wildlife monitoring seeks to provide accurate and precise inferences on population parameters across space and time for target species. Quantifying population parameters is essential for tracking biodiversity trends (Ledger et al., 2023), evaluating extinction risks (Ceballos et al., 2017; Gobush et al., 2022; Humle et al., 2016), developing conservation plans (e.g., IUCN SSC Primate Specialist Group, 2020), and assessing the effectiveness of management actions (Nichols & Williams, 2006; Palm et al., 2020). However, estimating population parameters, especially population density or abundance, presents major challenges for many species, particularly those that cannot be directly sampled due to their elusive behavior or limited visibility in the landscapes they inhabit (Laing et al., 2003; Pandong et al., 2018; Plumptre, 2000).

The gold standard for estimating abundance is through mark–recapture methods in which animals are captured, marked (e.g., with ear tags), and resighted or recaptured on subsequent sampling occasions (Otis et al., 1978; Pollock, 1976). However, such methods are costly in terms of time and effort. Thus, estimating abundance through mark–recapture is not feasible for many species and systems. Consequently, there are a number of methods to estimate abundance using “unmarked” count data in which animals are not individually identifiable including N-mixture (Royle, 2004) and distance sampling (Buckland, 2001) models. These methods account for individuals missed during sampling by estimating detection probability from either repeated sampling or ancillary distance measurements. While less effort-intensive than mark–recapture, unmarked methods still require direct observations of animals, which can be difficult to obtain for elusive species (Lollback et al., 2015; Pandong et al., 2018) and those that inhabit landscapes with limited visibility such as dense forests (Ahrestani et al., 2018; Laing et al., 2003; Marques et al., 2001).

Species that are difficult to directly observe can be monitored using indirect signs such as dung, tracks, or nests (Gusset & Burgener, 2005; Laing et al., 2003; Morgan et al., 2016). Distance sampling is the most common method for indirect sign data and involves counting the number of signs along transects and measuring distances to the observed signs (e.g., Kouakou et al., 2009; Kühl et al., 2017; Mohanarangan et al., 2022; Piel et al., 2015). Indirect sign methods have been used to estimate the population density of many terrestrial mammals, including ungulates (Jung & Kukka, 2016; Marques et al., 2001; Twahirwa et al., 2023), elephants (Meier et al., 2021; Twahirwa et al., 2023), and apes (Kouakou et al., 2009; Kühl et al., 2017; Rainey et al., 2010; Spehar et al., 2010). To obtain inferences using indirect sign data, surveys are

typically conducted using a systematic or randomized protocol (e.g., through distance sampling) with a model fit to the data to estimate sign density. Sign density is then converted to animal density via conversion factors (Cappelle et al., 2019; Hedges et al., 2012; Kuehl et al., 2007). Conversion factors require data on (1) the sign decay rate, which is estimated by collecting information on the duration that signs remain visible in the field (Laing et al., 2003; Morgan et al., 2016; Plumptre & Reynolds, 1996) and (2) the sign production rate, which is obtained by observing groups of animals in the field or enclosures to estimate the number of signs produced within a defined time interval (Mohanarangan et al., 2022; Plumptre & Harris, 1995; Wing & Buss, 1970). Indirect sign surveys are typically obtained using one of two methods: the standing crop sign count and the marked sign count (Plumptre & Reynolds, 1996). The standing crop sign count requires only one survey visit and relies on a priori knowledge of sign decay and production rates to convert sign density to animal density, as the time period over which signs are produced is unknown and inestimable using a single survey (Plumptre & Reynolds, 1996). However, sign decay rates vary across seasons and sites, representing a significant limitation of the standing crop sign count method (Bessone et al., 2021; Hedges et al., 2012; Kuehl et al., 2007; Plumptre & Harris, 1995). The marked sign count offers a solution: sites are visited on at least two occasions, removing the need to estimate the sign decay rate a priori, provided the interval is sufficiently short that fresh signs do not disappear between the first and second visit (Hashimoto, 1995; Plumptre & Reynolds, 1996). During the first visit, all existing signs of the species are marked; subsequent visits record the number of new signs produced. The number of signs produced over a known time interval is then used with a sign production rate (which still must be obtained from the literature or ancillary data) to calculate animal density.

While the marked sign count is an effective method to estimate the abundance of difficult-to-observe species, it involves discarding data from the first visit because the duration over which the original signs have been visible is unknown. Although discarding these data is standard protocol for the marked sign count method, it represents a loss of information because data from the first visit inform the long-term habitat use of the species, while data from subsequent visits describe the current species distribution (Spehar et al., 2010). For example, elephant dung observed during the first visit is estimated to be visible for 75–147 days on average (Nchanji & Plumptre, 2001), while the mean decay rates for chimpanzee nests varied between 37 and 91 days (Kouakou et al., 2009; Plumptre & Reynolds, 1996). Thus, harnessing the

information in both visits through a joint likelihood may improve the estimation of covariate effects on the abundance and prediction of spatial abundance patterns.

Another limitation of indirect sign methods is their typical reliance on conventional distance sampling, which does not account for spatial variation in animal density (Kéry & Royle, 2016). Under conventional distance sampling, population density estimates are positively biased if transects sample multiple habitats that host differing population densities (Fewster et al., 2009). Variance estimators based on post-stratification have been developed to minimize positive bias under maximum likelihood inference (Fewster, 2011; Fewster et al., 2009). An alternative to conventional distance sampling is hierarchical distance sampling, which allows variation in density to be explicitly modeled with covariates, an important objective for characterizing species' ecological niches (De La Fuente et al., 2021), predicting the impacts of environmental change (Waldock et al., 2022), mapping spatial variation in density (Miller et al., 2013), and informing conservation prioritization and management (Johnston et al., 2015).

Here, we describe a modified hierarchical distance sampling model that accommodates spatial variation in sign density using the information from all visits of the marked sign count data to estimate model parameters, rather than discarding data from the first sampling event. We apply our modeling framework to populations of eastern chimpanzees (*Pan troglodytes schweinfurthii*) and African savanna elephants (*Loxodonta africana*) that inhabit Maramagambo and Kalinzu Forest Reserves in Western Uganda. Eastern chimpanzees are listed as endangered on the IUCN Red List (Humble et al., 2016). Their populations are declining throughout most of their range due to habitat loss, pet trade, bushmeat, diseases, and climate change (Humble et al., 2016; Plumptre, 2010). African savanna elephants are also classified as endangered (Gobush et al., 2022) due to range contraction of more than 50% since the 1940s, habitat loss, poaching for ivory, and climate change. Given the declining population trends of these species, estimates of abundance across space and time are urgently needed to inform local conservation actions. Both species are difficult to directly observe in forests and are instead surveyed using indirect signs, as chimpanzees construct nests for sleeping each night and elephants produce large dung piles. These indirect signs (i.e., nests and dung) remain visible for several days to months, depending on decay rates, and have a higher chance of being detected than the animals themselves (Morgan et al., 2016; Nchanji & Plumptre, 2001). The data for our analyses come from transects that were surveyed in 2007 and again in 2021. Our objective is to improve the estimation of expected density by combining

visit one, and subsequent visit data through partially shared covariate effects in a joint likelihood. Additionally, we illustrate the limitations of existing approaches for analyzing indirect survey data while providing an easy-to-implement alternative. Specifically, we aim to demonstrate how our framework can be used to estimate precise spatiotemporal patterns of population density. We conclude by providing recommendations on best practices for using indirect count data in population analyses.

METHODS

Study area and species

Our study was conducted in Maramagambo Forest Reserve (0°26'50.87" S, 29°54'11.98" E) and Kalinzu Forest Reserve (0°23'47.73" S, 30° 3'42.17" E) within Queen Elizabeth Conservation Area in western Uganda (Figure 1). The two forest reserves are contiguous and cover an area of 580 km² (Maramagambo: 443 km²; Kalinzu: 137 km²). Maramagambo is dominated by semi-deciduous forest with thickets at the edges and lies on the Albertine Rift floor 915–1250 m above sea level, while Kalinzu is a moist evergreen forest and lies on the Rift escarpment 1250–1845 m above sea level (Howard, 1991). The region experiences a tropical climate characterized by two wet (March–May and September–November) and two dry (June–August and December–February) seasons, with annual rainfall and temperature ranging between 1150–1400 mm and 14–28°C, respectively (Hashimoto et al., 1999; Howard, 1991). A total of 58 mammal species have been recorded in our study area (Plumptre et al., 2007), including eight primate species. Some of the threatened large mammal species that occur in these forest reserves include chimpanzees, L'hoest's monkey (*Cercopithecus lhoesti*), African savanna elephants, leopard (*Panthera pardus*), African golden cat (*Caracal aurata*), and hippopotamus (*Hippopotamus amphibius*). Maramagambo Forest forms part of the Queen Elizabeth National Park and the northern and southern boundaries are contiguous with savanna woodland forming an extensive protected area system (>2500 km²).

Data collection

We conducted indirect surveys of chimpanzees (nests) and elephants (dung) in Maramagambo and Kalinzu Forest Reserves following a distance sampling methodology in September–November 2007 and January–March 2021 (Figure 1). However, elephants and their dung were

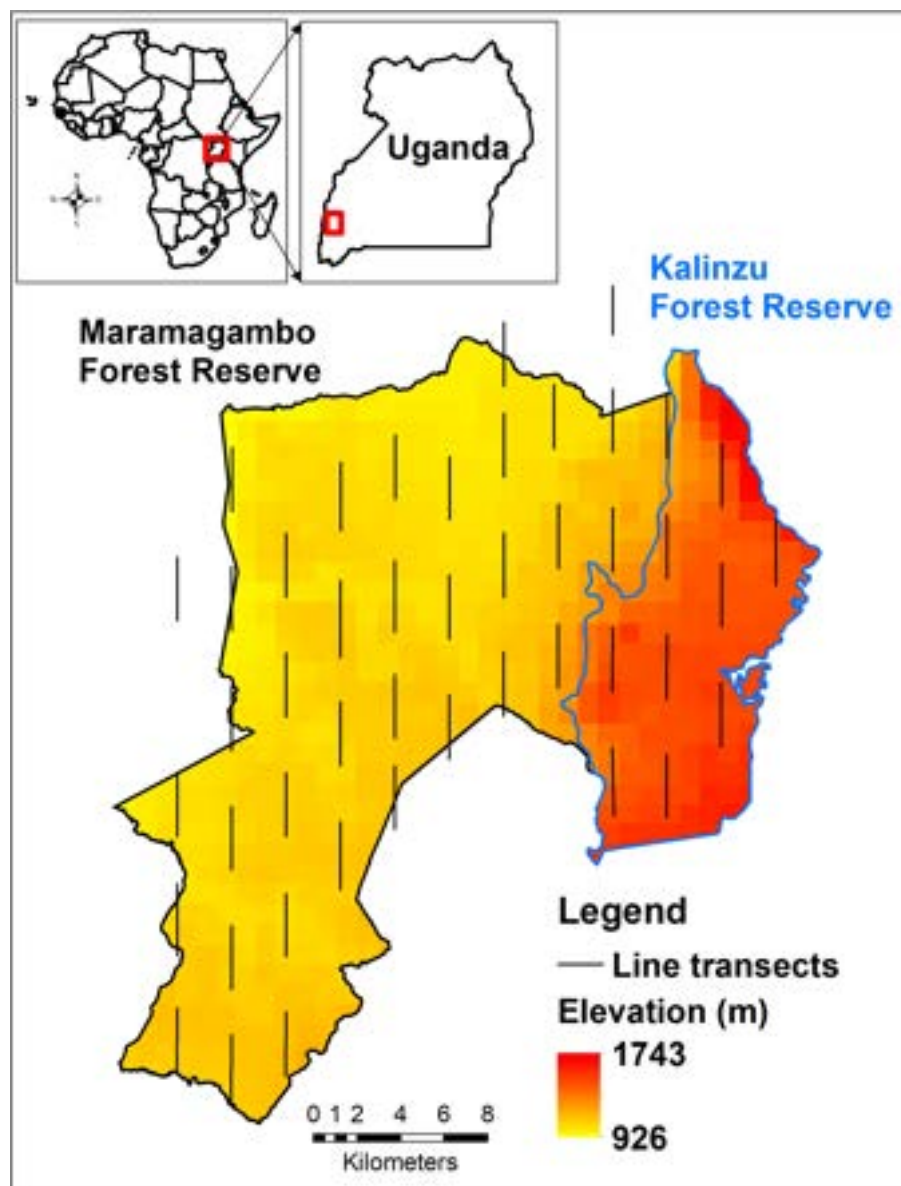


FIGURE 1 Map of the study area and line transects used to survey indirect signs (i.e., three visits ~25 days apart on average) of chimpanzee and elephant populations across an elevation gradient within two contiguous forest reserves in western Uganda during the 2007 and 2021 surveys.

not observed in Kalinzu Forest Reserve in either of the two survey periods. We established forty-six 3-km line transects with a spacing of 2.5 km following a systematic random sampling design using Distance 5.0 (Thomas et al., 2010). Transects were established in 2007 (WCS & MUIENR, 2008) and resurveyed in 2021. Transects were sampled three times per survey period following a marked sign count approach. Data from the first visit (Visit 1) of the marked sign count are equivalent to data collected using the standing crop method, which we deemed inappropriate for our application because the sign decay rate in the study area was unknown a priori. Of the 46 line transects, 36 were in Maramagambo Forest

Reserve and 10 were in Kalinzu Forest Reserve (Figure 1). Transects were cut through the forest following a north compass direction three weeks before data collection to minimize disturbance to animals. The surveys were conducted by experienced field research assistants who had been previously involved in surveying large mammals in the Albertine Rift region (Plumptre et al., 2003). Four survey teams, consisting of three people each, collected data on the signs of the presence of chimpanzees (nests) and elephants (dung) starting in the morning (~7:00 am). Field assistants walked the transects at a speed of approximately 1 km per hour. Distance measurements to chimpanzee nests were recorded in meters

using a rangefinder or tape measure, while distances to elephant dung were recorded in centimeters using a tape measure. The average time between replicate surveys during each field campaign was 25 days (SD = 2.5, range 20–33), which was short enough to ensure that no chimpanzee nests or elephant dung would have decayed between visits (Nchanji & Plumptre, 2001; Plumptre & Reynolds, 1996). Chimpanzee nests and elephant dung piles were marked by attaching a ribbon to an adjacent tree/sapling. Finally, we obtained elevation data (spatial resolution: 90 m × 90 m) across the study area to use as a predictor variable in our analyses (Farr & Kobrick, 2000). To account for variation in elevation along the length of the line transect, we resampled elevation data to 1 km² and obtained elevation values for the midpoint of the 3-km transect. Elevation strongly covaries with annual mean temperature and precipitation, which are known to influence the distributions of the focal species across their ranges (Carvalho et al., 2021; Jiang et al., 2020).

Modeling approach

Overview

We applied conventional and hierarchical distance sampling models to assess the status of chimpanzee and elephant populations in 2007 and 2021 (Table 1), by converting sign density (chimpanzee nests; elephant dung) into animal density using production rates from the literature and the number of days between the first and last survey visits. Distance sampling is widely used to estimate the density of wildlife populations and can be applied to either direct or indirect observations of

animals (Buckland, 2001; Miller, Pacifici, et al., 2019; Miller, Rexstad, et al., 2019). We assumed that each adult chimpanzee builds 1.09 nests a day (Plumptre & Reynolds, 1997) and that each elephant produces 17 dung piles per day (Wing & Buss, 1970). Sign production rates are less variable than decay rates, and thus using rates from the literature is common practice (e.g., Kouakou et al., 2009; Nchanji et al., 2008; Sanz, 2004).

The assumptions underlying distance sampling are that objects on the transect are observed with perfect detection (i.e., when distance = 0), transects are placed at random, objects are detected at their original location, and distance measurements are recorded without error (Buckland, 2001). For line transect distance sampling, the effective strip width within which observations are made enables the estimation of the area sampled, which is important in calculating sign (and hence animal) density in the surveyed area. Indirect observation data are typically analyzed using conventional distance sampling approaches (e.g., Kouakou et al., 2009; Mohanarangan et al., 2022; Piel et al., 2015; Spehar et al., 2010; Wanyama et al., 2010). The drawback of conventional distance sampling is that it does not account for variation in density among transects (Kéry & Royle, 2016). In addition, encounter rate variance (i.e., variation in the number of objects detected per transect) influences the precision of density estimates, especially when there are considerable differences in the spatial distribution of animals in the study area (Buckland et al., 2004; Fewster et al., 2009). To model spatial variation in density among transects, we adopted a hierarchical distance sampling model—an extension of conventional distance sampling that allows the inclusion of covariates that account for variation in density among transects (Kéry & Royle, 2016).

TABLE 1 Capabilities of the models employed: Models were fitted using either Bayesian or maximum likelihood (ML) inference.

Outputs	ML	Bayesian inference		
	Conventional distance sampling	Conventional distance sampling	Hierarchical distance sampling	Modified hierarchical distance sampling
Realized density	✓	✓	✓	✓
Expected density			✓	✓✓
Effect of covariates			✓	✓✓
Sign decay rates				✓✓
Change in population	✓	✓	✓	✓
Spatial prediction			✓	✓✓
Temporal prediction			✓	✓✓

Note: Checkmarks identify the capabilities of a model, while the double checkmarks identify cases in which the modified hierarchical distance sampling model outperformed simpler versions in the case studies. Realized density is estimated, assuming the count of signs as fixed (i.e., no random variation) while expected density is estimated as a function of covariates.

The marked sign count method involves collecting indirect sign data across multiple visits (in our study, three visits). Data from the first visit describe the distribution and abundance patterns of the target species over a longer term, but unknown, time frame; data from subsequent visits describe the distribution and abundance patterns over a shorter, known time frame. The standard approach of analyzing marked sign count data involves discarding data from the first visit. As such, inference on spatial variation in abundance using the standard approach is informed by only the short-term distribution of the species. We thus modified our approach to include data collected during the first visit via a joint likelihood (of the hierarchical distance sampling model) in which some parameters are shared between the first and subsequent visits (Figure 2). Our modified model uses data from all visits to improve density estimation; the model includes partially linked abundance submodels (i.e., separate intercepts but shared covariate effects) and independent observation submodels between Visit 1 and Visits 2–3 (Figure 2).

Conventional distance sampling using marked sign data

In conventional distance sampling, realized animal density across the study area, $\hat{D}$, is assumed to be a function of the number of signs, c_j , detected along the line transect j , the total area surveyed a , the average probability of detection of signs within the surveyed region $\bar{p}$, the sign production rate (i.e., conversion factor from sign to animal density) r , and the time interval (i.e., conversion factor) between the first, second, and third visits t :

$$\hat{D} = \frac{\sum c_j}{a \bar{p} r t}. \quad (1)$$

The time interval is calculated by summing the average number of days that signs remained visible between Visits 1 and 2, and Visits 2 and 3. We estimate $\bar{p}$ using a half-normal detection function $g(x)$ that describes the probability of detecting a sign (i.e., nests, dung) conditional on perpendicular distance x from the line transect:

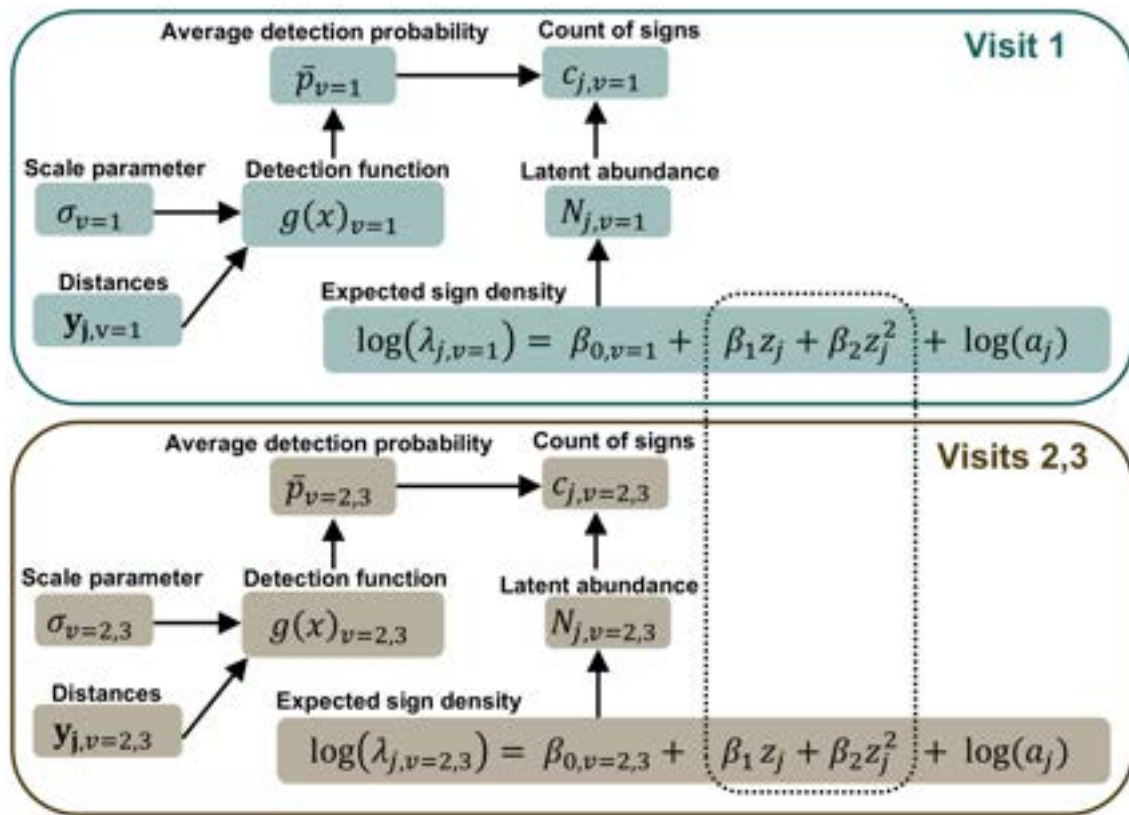


FIGURE 2 Modified hierarchical distance sampling model with shared covariate effects across all visits. Subscript $v = 1$ and $v = 2, 3$ indicate whether model parameters are associated with either Visit 1 or Visits 2–3 of the marked sign count data, while j indexes transect. y_j are the observed distances to signs, σ is the scale parameter, which determines how rapidly detection probability declines with distance, $g(x)$ is the detection function, $\bar{p}$ is the average detection probability across the surveyed area, c_j is the count of signs, N_j is the true (latent) number of signs, λ_j is the expected density of signs, β_0 is an intercept, β_1 and β_2 are the linear and quadratic effects of elevation z_j on expected sign density, and a_j is the area surveyed by transect j . Shared parameters are shown with a dashed box.

$$g(x) = \exp\left(\frac{-x^2}{2\sigma^2}\right), \quad (2)$$

where σ is a scale parameter that determines how quickly detectability decays over distance x . The average detection probability $\bar{p}$ is derived using the following equation:

$$\bar{p} = \int_0^w g(x)[x^*]dx, \quad (3)$$

where w is the effective strip width within which observations were made, $[x^*]$ is the probability distribution of observed distances, which is equal to $\frac{1}{w}$, assuming random placement of transects with respect to the signs. The integral of Equation (3) is solved by specifying a probability density function $f(x)$ of observed perpendicular distances to estimate parameters of $g(x)$:

$$f(x) = \frac{g(x)}{\int_0^w g(x)dx}. \quad (4)$$

We fit conventional distance sampling models using both maximum likelihood (Distance in R; Miller, Pacifici, et al., 2019) and Bayesian inference (JAGS; Plummer, 2003, jagsUI package in R; Kellner, 2021). For Bayesian inference, we used Uniform (1, 25) and Uniform (1, 5) priors for the scale parameter σ for chimpanzees and elephants, respectively. The bounds of the uniform priors were substantiated with a prior predictive check to visualize the implied relationships between detection probability and distance, and to assess whether these relationships were biologically reasonable (Appendix S1: Figure S1). For maximum likelihood inference, we used three encounter rate variance estimators that reduce bias in density estimates: (1) overlapping strata (O2) and (2) nonoverlapping strata (S2) that have been developed for systematic line transect designs, and (3) a random design-based estimator (R2) that performs well for both random and systematic designs when objects are distributed uniformly in space (Fewster et al., 2009; Appendix S1: Figure S2). We defined strata as spatially adjacent transect pairs, which are grouped together in a post-stratification process under the assumption that such groupings have similar spatial patterns of animal density (Fewster et al., 2009).

Hierarchical distance sampling model using marked sign data

Hierarchical distance sampling models estimate the average probability $\bar{p}$ of detecting objects within the surveyed

area by integrating the detection function $g(x)$ across all distance measurements in relation to the probability density of x , $[x^*]$, as specified in Equation (3). We estimated $g(x)$ by modeling the relationship between perpendicular distance measurements from the line transect to signs (i.e., nest, dung), assuming a half-normal detection function as specified in Equation (2). To estimate the average detection probability, $\bar{p}$, we classified distance measurements into distance classes ($h = 1, 2, \dots, H$) with class width k and distance breaks $[b_0, b_1], [b_1, b_2], \dots, [b_{H-1}, b_H]$ to enable implementation in a Bayesian framework (Kéry & Royle, 2016). We computed detection probability for distance class h and transect j , p_{hj} , by numerically integrating the detection function $g(x)$ from the distance class's first break point b_{h-1} to its second break point b_h , adjusted by distance class width k :

$$p_{hj} = \frac{\int_{b_{h-1}}^{b_h} g(x)dx}{k}. \quad (5)$$

The number of distance measurements within each distance class at transect j , $\mathbf{y}_j$ (bolded to denote that it is a vector), follows a multinomial distribution:

$$\mathbf{y}_j \sim \text{Multinomial}(c_j, \mathbf{p}_j^*), \quad (6)$$

where c_j is the total number of observed signs at line transect j , that is, $c_j = \sum_h y_{hj}$ and $\mathbf{p}_j^*$ is a vector of conditional cell probabilities, that is, the probability that an object is within distance class h . Conditional cell probabilities must sum to 1 and thus $\mathbf{p}_j^* = \frac{p_{hj}}{\sum_h p_{hj}}$. Next, the total number of observed signs on a transect, c_j , follows a binomial distribution with parameters N_j (the true number of signs at line transect j) and $\bar{p}$, the average detection probability of an object within the sampled area, calculated as $\bar{p} = \sum_h p_{hj}$:

$$c_j \sim \text{Binomial}(N_j, \bar{p}). \quad (7)$$

True abundance of signs N_j at each line transect j is modeled as a negative binomial distribution fitted as a Poisson–gamma mixture:

$$N_j \sim \text{Poisson}(\rho_j \lambda_j), \quad (8)$$

where ρ_j controls for overdispersion and is modeled as a draw from a gamma distribution. We modeled expected sign density λ_j as a function of covariates using a log-link function:

$$\log(\lambda_j) = \beta_0 + \beta_1 z_j + \beta_2 z_j^2 + \log(a_j), \quad (9)$$

where β_0 is the intercept, β_1 is the linear effect of elevation z_j , β_2 is the quadratic effect of elevation, and a_j is the area surveyed by transect j . We standardized elevation to have a mean of 0 and SD of 1.

We fit our models using R (R Core Team, 2023) and JAGS (Plummer, 2003) software with the jagsUI package (Kellner, 2021). We ran three parallel chains for 60,000 iterations with a burn-in of 10,000 iterations and thinning rate of 10 to obtain 15,000 posterior samples. We used Normal (0, 10) priors for parameters β_0 , β_1 , and β_2 , and Uniform (1, 25) and Uniform (1, 5) priors for the scale parameter σ for chimpanzees and elephants, respectively. We assessed convergence by visually inspecting trace plots and checking that the convergence diagnostic $\hat{R} < 1.1$ (Gelman, 2004).

Modeling innovation: Modified hierarchical distance sampling model using marked sign data from all sampling events

Our modified hierarchical distance sampling model combines data from the first visit of the marked sign count method and all subsequent visits by linking parameters in a joint likelihood for the abundance model and estimating separate observation models (Figure 2).

We estimated the expected density of signs (i.e., chimpanzee nests, elephant dung) with separate intercepts for the first and subsequent visits while covariate effects (i.e., elevation) were shared across visits. In the equations below, v indexes visit:

$$\log(\lambda_{j,v=1}) = \beta_{0,v=1} + \beta_1 z_j + \beta_2 z_j^2 + \log(a_j), \quad (10)$$

$$\log(\lambda_{j,v=2,3}) = \beta_{0,v=2,3} + \beta_1 z_j + \beta_2 z_j^2 + \log(a_j), \quad (11)$$

where $\lambda_{j,v=1}$ is the expected density of signs for Visit 1, $\lambda_{j,v=2,3}$ is the expected density of signs for Visits 2–3, $\beta_{0,v=1}$ is the intercept for Visit 1, $\beta_{0,v=2,3}$ is the intercept for Visits 2–3, β_1 and β_2 are the linear and quadratic effects of elevation z_j that are shared across the two equations, and a_j is the area surveyed by transect j .

The number of days in which signs have been visible during the first visit (i.e., decay rate) is an important parameter in the estimation of animal density following the application of a standing crop method to carry out surveys (Bessone et al., 2021; Kuehl et al., 2007; Morgan et al., 2016) and assessing the impacts of climate change

(Bessone et al., 2021). We estimated the mean number of days (i.e., decay rate) over which signs observed during Visit 1 of the marked sign count data (i.e., equivalent to standing crop data) were visible using the modified hierarchical distance sampling model. We assumed that population density remained unchanged between Visit 1 and Visits 2–3. Sign decay rates are traditionally estimated in the field by collecting information on the duration required for the signs to decay (Laing et al., 2003; Morgan et al., 2016; Plumptre & Reynolds, 1996). Given that both the standing crop (i.e., Visit 1) and marked sign counts produce similar density estimates (Kouakou et al., 2009), we derived the duration (S ; in days) over which signs remained visible after Visit 1 using the following equation:

$$S = \frac{N_{v=1}}{D_{v=2,3} r a}, \quad (12)$$

where $N_{v=1}$ is the total number of signs across transects observed during Visit 1 corrected for imperfect detection, $D_{v=2,3}$ is the realized density of animals per square kilometer from Visits 2–3, and is estimated using Equation (1), r is the sign production rate, and a is the sum of the areas of all the transects. Unlike the traditional model, the modified hierarchical distance sampling model allows the estimation of sign decay rates for the first visit in the analysis of marked sign count data.

All parameters in our modified model were estimated using Bayesian inference with R and JAGS and weakly informative priors as specified in the previous section. We calculated the average population sizes for chimpanzees and elephants for the 2007 and 2021 surveys by multiplying the estimated local realized densities by the area (in square kilometers) of the forest reserves. We predicted the expected density of chimpanzees and elephants across the study area in 2007 and 2021 using Equation (11) and estimated the change in local population density by subtracting 2007 predicted density from the 2021 predicted density using the R package raster (Hijmans, 2023). In a post hoc analysis across time, we summarized the posterior distribution of differences to estimate the probability that a change in population density had occurred at specific percentages (e.g., 5%, 10%, 30%). First, we estimated the percentage change in realized density (e.g., 10%) using 2007 as the base year, and then computed the proportion of posterior samples greater or less than the estimated value to obtain a probability of a change in population density (R Core Team, 2023). In the results below, we report the means and 95% credible intervals (95% CIs) of model estimates.

Evaluating bias and precision

The relative bias between the expected and observed signs of chimpanzees and elephants for the hierarchical and modified hierarchical distance sampling models was evaluated using leave-one-out cross-validation. Sign count data for one transect was omitted, and then we fit the models using the remaining transects (Appendix S1). We estimated relative bias across the omitted transects using the following equation:

$$\text{Relative bias} = \frac{\sum (\text{expected signs per transect} - \text{observed signs per transect})}{\sum (\text{observed signs per transect})} \quad (13)$$

We report coverage (i.e., measure of whether the 95% CI for the predicted expected sign count contains the observed value). We assessed the precision of expected density estimates from the hierarchical and modified hierarchical distance sampling models by plotting the effect of covariates obtained using Visit 1 data, Visits 2–3 data, and Visits 1–3 data.

RESULTS

Expected and realized density

We estimated both expected and realized density (Efford & Fewster, 2013; Royle et al., 2013) of chimpanzees and elephants in the study area (Table 2). Expected density was estimated as a function of covariates (Equations 9 and 11 for the hierarchical and modified hierarchical models), assuming that the sign counts are drawn from a probability distribution, whereas realized

density was estimated assuming that the sign counts are fixed (i.e., no distribution assumption using Equation 1 for all three model types). The results show that expected density estimates obtained from a modified hierarchical distance sampling model are more precise compared with the hierarchical distance sampling model estimates (Table 2). However, the realized density estimates were more similar for conventional, hierarchical, and modified hierarchical distance sampling models (Appendix S1: Table S1).

We compared density estimates (realized and expected) of chimpanzees and elephants from conventional, hierarchical, and modified hierarchical distance sampling approaches across space (Figure 3). Conventional distance sampling can only estimate density at the sampled transects (Figure 3a,b). In contrast, the hierarchical distance sampling models can be used to predict density across the study area (Figure 3c,d). The standard hierarchical distance sampling model (which includes data from Visits 2–3 only) generally predicted lower densities of chimpanzees but higher densities of elephants compared with the modified hierarchical distance sampling model (which includes data from all visits).

Bayesian implementation of the conventional distance sampling model produced more precise estimates than any of the maximum likelihood estimators (Figure 4). As a result, the population density estimates for both chimpanzees and elephants across the two survey periods were more precise for all models fitted using Bayesian inference compared with the maximum likelihood estimate obtained using the default variance estimator (Appendix S1: Table S1). The precision of density estimates from the maximum likelihood implementation of conventional distance sampling varied—sometimes dramatically—according to the choice of the variance estimator (Figure 4).

TABLE 2 Expected and realized density as estimated from hierarchical (HDS) and modified hierarchical (MHDS) distance sampling models.

Site	Year	Expected density				Realized density			
		HDS	CV	MHDS	CV	HDS	CV	MHDS	CV
Chimpanzees									
MKFRs	2007	1.12	25.99	1.15	22.08	1.29	6.6	1.29	6.5
MKFRs	2021	1.15	24.79	0.86	21.05	0.94	7.5	0.94	7.4
Elephants									
MFR	2007	0.07	34.45	0.087	28.19	0.17	13.1	0.17	13.4
MFR	2021	0.65	22.8	0.58	20.66	0.57	7.3	0.57	7.4

Note: The sites are Maramagambo and Kalinzu Forest Reserves combined (MKFRs) and Maramagambo Forest Reserve (MFR). CV refers to the coefficient of variation.

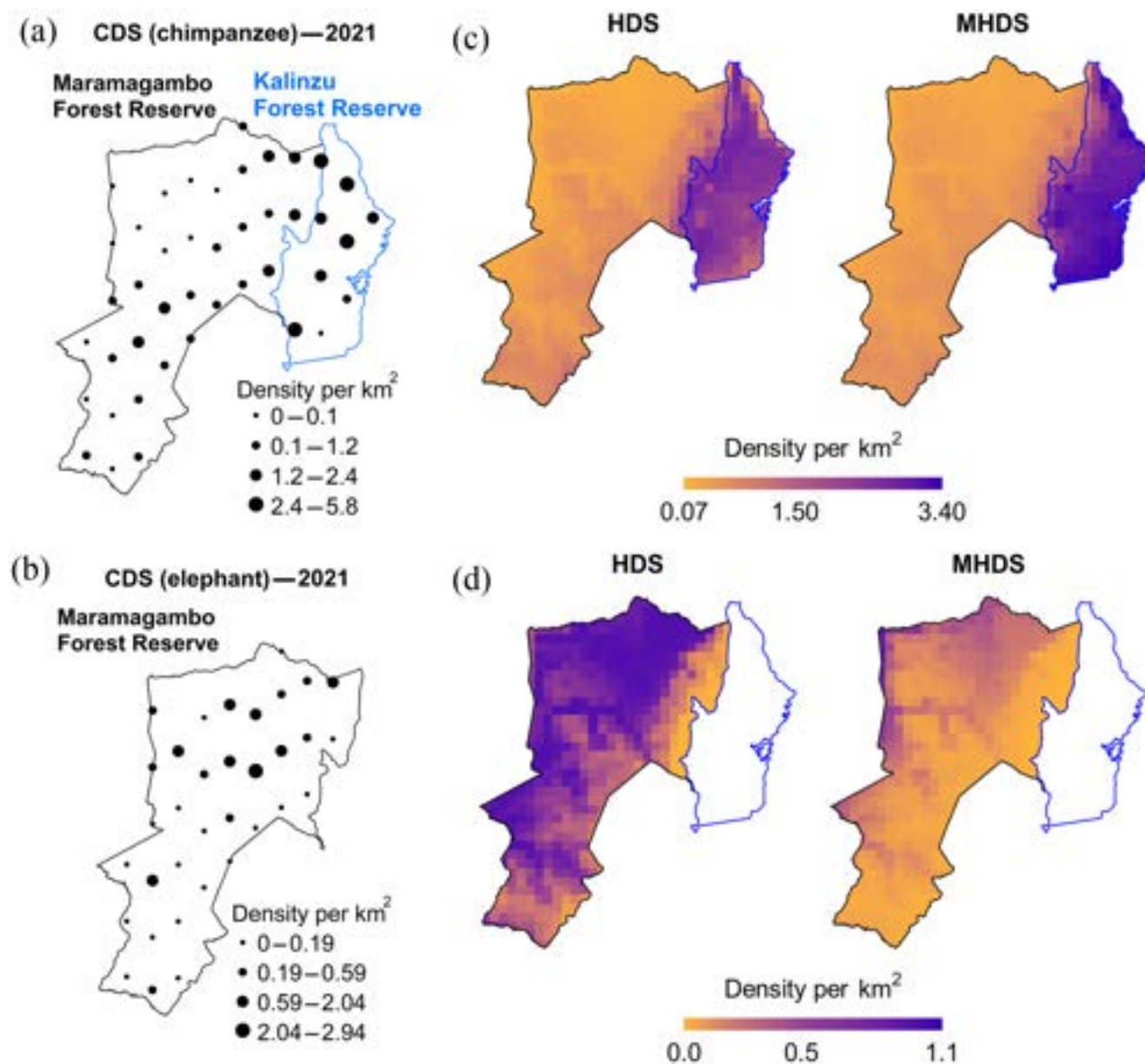


FIGURE 3 Spatial variation in density of (a–c) chimpanzees and (b–d) elephants in 2021 using conventional distance sampling (CDS) (a, b; Visits 2 and 3), hierarchical distance sampling (HDS) (c, d, left column; Visits 2 and 3 with elevation covariate), and the modified hierarchical distance sampling (MHDS) (c, d, right column; Visits 1–3 with elevation covariate). Chimpanzee estimates are for the Maramagambo and Kalinzu Forest Reserves, while elephant estimates are for Maramagambo Forest Reserve only. The modified hierarchical distance sampling (right column) shows spatial variation in density after accounting for both long-term (Visit 1) and recent patterns (Visits 2 and 3) of habitat use by chimpanzees and elephants.

Model validation: Modified hierarchical distance sampling model

The estimated bias between expected and observed sign densities for chimpanzee and elephant populations showed a similar pattern of underfitting or overfitting for the hierarchical and modified hierarchical distance sampling models across transects (Figure 5a; Appendix S1: Figures S3 and S4). The relative bias of sign density was

−0.17% (i.e., 2021 survey) and −0.36% (i.e., 2007 survey) for hierarchical distance sampling, and −0.21% (i.e., 2021 survey) and −0.14% (i.e., 2007 survey) for the modified hierarchical distance sampling for chimpanzees. For elephants, the relative bias of sign density was 0.21% (i.e., 2021 survey) and 0.13% (i.e., 2007 survey) for hierarchical distance sampling, and −0.12% (i.e., 2021 survey) and 0.07% (i.e., 2007 survey) for the modified hierarchical distance sampling for

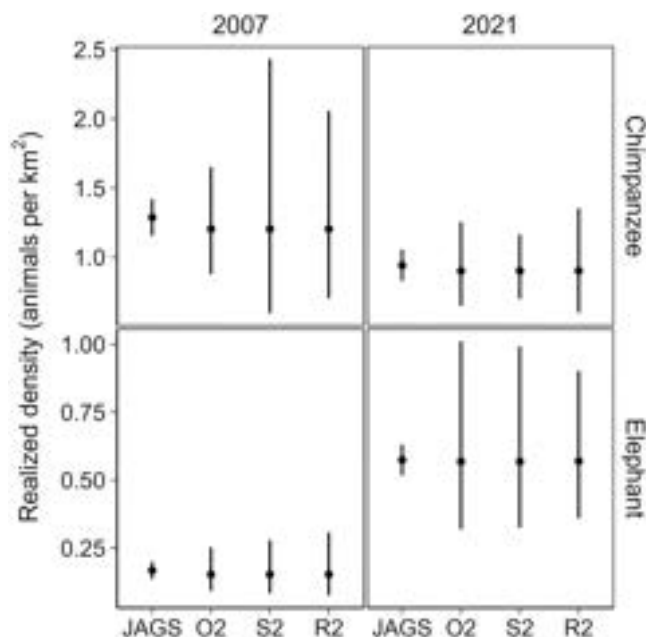


FIGURE 4 Realized density estimates for chimpanzees and elephants (2007 and 2021 surveys), averaged across the study area using conventional distance sampling (Visits 2 and 3). JAGS indicates estimates generated using Bayesian inference (i.e., conventional, hierarchical, and modified hierarchical distance sampling models), while O2, S2, and R2 show maximum likelihood inferences using different encounter rate variance estimators. Points represent the mean values, while the thin vertical lines show the 95% credible and confidence intervals for Bayesian and maximum likelihood inferences, respectively. O2 and S2 variance estimators are based on post-stratification and have been developed for systematic line transect designs, while R2 is based on random transect designs. Chimpanzee estimates are shown for the Maramagambo and Kalinzu Forest Reserves, while elephant estimates are for Maramagambo Forest Reserve only.

chimpanzees. The 95% CI contained the observed value for all the models and years (Appendix S1: Figures S3 and S4). The modified hierarchical distance sampling modeling integrates the variability in sign abundance across space and time, resulting in expected density estimates that are intermediate between Visit 1, and Visits 2 and 3 (Figure 5b; Appendix S1: Figures S5–S7).

Density estimates from the modified hierarchical distance sampling model

The modified hierarchical distancing sampling model that included all sampling events (i.e., Visits 1–3) provided inferences that were not possible using either conventional or hierarchical distance sampling that used data only from Visits 2 to 3 (Table 1). First, the modified hierarchical distance sampling model estimated more

precise covariate effects on expected animal density (compared with the standard hierarchical distance sampling model) using data from all visits (Figure 6). For example, the coefficient of variation (i.e., the ratio of the SD to the mean) for the linear effect of elevation on chimpanzee nest density in 2007 was 14% versus 18% for the modified hierarchical versus standard hierarchical models. Similarly, the coefficient of variation for the linear effect of elevation on elephant dung density in 2007 was 15% versus 27% for the modified hierarchical versus standard hierarchical models. Second, combining the two datasets (i.e., Visit 1 and Visits 2–3) in the same modeling framework enabled estimation of the number of days that signs collected during the first visit were visible. We estimated that chimpanzee nests were visible for 66 days (95% CI: 54, 80) and 90 days (95% CI: 76, 105), while elephant dung was visible for 30 days (95% CI: 23, 38) and 253 days (95% CI: 188, 332) for the 2021 and 2007 surveys, respectively (Tables 3 and 4).

Population status and change (2007, 2021)

Chimpanzee realized density was higher in Kalinzu than in Maramagambo in both years (Table 3). For Kalinzu, we estimated a realized density of 3.74 (95% CI: 3.19, 4.4) individuals per square kilometer in 2007 and 2.71 (95% CI: 2.23, 3.3) in 2021, translating to approximately 512 (95% CI: 437, 603) individuals in 2007 and 371 (95% CI: 306, 452) individuals in 2021. The probability that the population of chimpanzees in Kalinzu declined by 10% was 0.95. In Maramagambo, we estimated chimpanzee realized density of 0.59 (95% CI: 0.46, 0.74) in 2007 and 0.44 (95% CI: 0.37, 0.55) in 2021, or an estimated population size of 261 (95% CI: 204, 328) individuals in 2007 and 195 (95% CI: 164, 244) in 2021. The probability that chimpanzee density in Maramagambo had declined by at least 10% was 0.84 (Table 3). The biggest losses in chimpanzee expected density from 2007 to 2021 were estimated to have occurred along the Kalinzu–Maramagambo border (Figure 7). In 2007, chimpanzee expected density increased with elevation until 1310–1380 m, at which point it began declining (Figure 6). In contrast, for the 2021 survey, chimpanzee expected density showed a monotonic increase with elevation (Figure 6).

We estimated a realized density of 0.17 (95% CI: 0.13, 0.21) elephants per square kilometer in 2007 and 0.57 (95% CI: 0.49, 0.66) in 2021 for Maramagambo, translating to 75 (95% CI: 58, 93) and 253 (95% CI: 217, 292) individuals in 2007 and 2021, respectively (Table 4). We estimated a 0.94 probability that population density of elephants had increased by at least 100% (~75 individuals, Table 4). The largest increase in elephant expected

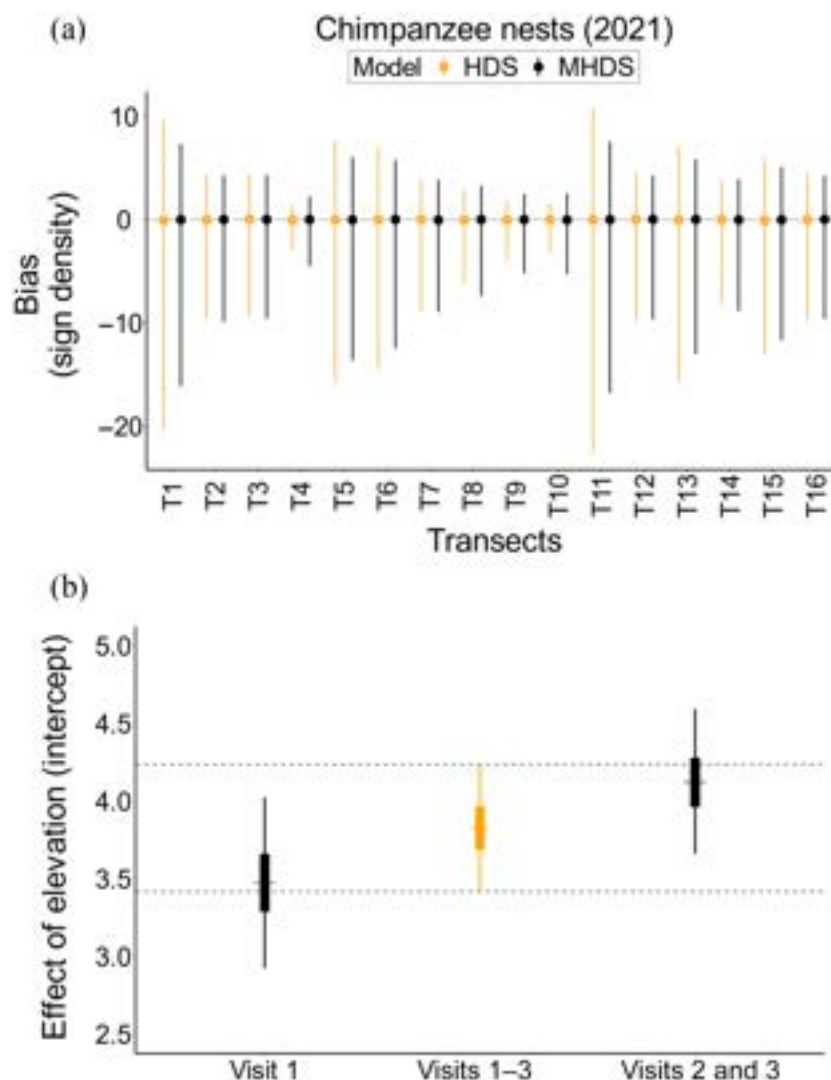


FIGURE 5 (a) Estimated bias in sign density per transect and (b) effect of covariates (log scale) on expected sign density of chimpanzees. Hierarchical distance sampling (HDS) and modified hierarchical distance sampling (MHDS) indicate model results from hierarchical and modified hierarchical distance sampling models, respectively. Modified hierarchical distance sampling model (Visits 1–3) characterizes both short-term and long-term patterns of habitat use as reflected in covariate effects intermediate between those estimated by models using Visit 1 or Visits 2 and 3 data.

density was observed toward the western boundary of Maramagambo that borders Queen Elizabeth National Park (Figure 7). For both the 2007 and 2021 surveys, elephant expected density decreased with elevation monotonically (Figure 6). The areas with the greatest changes were determined by visual inspection of maps and referencing the legend to assess the magnitude of change.

DISCUSSION

We extended indirect sign methods to improve inference on population parameters of elusive species by implementing a modified hierarchical distance sampling

model that uses data from all marked sign count visits (i.e., Visit 1 and Visits 2–3) to inform spatial variation in expected density of a focal species (Figure 2). The modified hierarchical distance sampling model improved the precision of covariate effects on expected sign density by accounting for both long-term (Visit 1) and recent patterns (Visits 2–3) of habitat use by chimpanzees and elephants (Figure 6). By partially sharing parameters in the ecological model, the model accounts for the variability in expected density across sites that neither of the individual models would be able to characterize. Our modeling approach is akin to data integration, which represents an improved way of estimating population parameters by linking submodels (Kéry & Royle, 2021;

Miller, Rexstad, et al., 2019; Zipkin et al., 2023). Additionally, incorporating Visit 1 data accounts for some of the variation due to zero inflation in habitat use observed in subsequent visit data (Dénes et al., 2015). In a similar vein, Pandong et al. (2018) developed a zero-inflated N-mixture model that used Visit 1 data as an indicator for orangutan habitat suitability while accounting for imperfect detection. Their results showed that incorporating Visit 1 data improved the precision and reliability of orangutan density estimates.

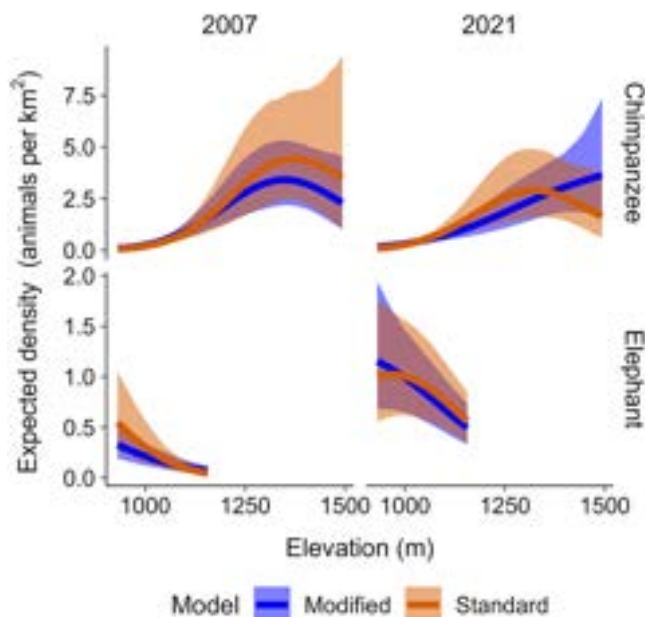


FIGURE 6 Effect of elevation on the expected density of chimpanzees and elephants for the 2007 and 2021 surveys estimated using the modified hierarchical model approach (blue; data from all three visits) and the standard approach (orange; data from only the second and third visits). Lines show means and the shaded areas show the 95% credible intervals. The modified approach improves the estimates of covariate effects on expected animal density by accounting for both the long-term (Visit 1) and recent patterns (Visits 2 and 3) of habitat use by chimpanzees and elephants.

TABLE 3 Realized density (mean and 95% CI), the probability of change by certain percentages of decrease between 2007 and 2021, and the number of days (mean and 95% CI) that signs of chimpanzees remained visible estimated using the modified hierarchical distance sampling model.

Site	Density		Probability of change				No. days	
	2007	2021	5%	10%	30%	50%	2007	2021
MKFRs	1.29 (1.13, 1.46)	0.94 (0.81, 1.09)	0.99	0.98	0.35	0	90 (76, 105)	66 (54, 80)
MFR	0.59 (0.46, 0.74)	0.44 (0.37, 0.55)	0.91	0.84	0.35	0.04	130 (98, 169)	58 (41, 79)
KFR	3.74 (3.19, 4.4)	2.71 (2.23, 3.3)	0.98	0.95	0.4	0.02	68 (55, 83)	72 (56, 91)

Note: MFR and KFR refer to Maramgambo and Kalinzu Forest Reserves, respectively, while MKFRs represent estimates for the two forest reserves combined.

Relative bias between the expected and observed sign densities of chimpanzees and elephants was minimal for both the hierarchical and modified hierarchical distance sampling models—suggesting that combining Visit 1 and Visits 2–3 does not bias parameter estimates (Figure 5a; Appendix S1: Figures S3 and S4). However, the increase in precision of covariate effects is due to the modified hierarchical distance sampling model integrating over spatial and temporal variation of Visit 1 and Visits 2–3 data—thus improving the model's predictive ability (Figure 5b; Appendix S1: Figures S5–S7).

Obtaining reliable estimates of population density for wildlife species is challenging, especially when using indirect count methods (Ahrestani et al., 2018; Wanyama et al., 2010). Under traditional analysis frameworks, detecting changes in population density between survey periods is challenging when using indirect count data due to a lack of precision (Piel et al., 2015; Plumptre, 2000; Wanyama et al., 2010). For example, a population change of even 30%–50% is unlikely to be detected when monitoring mammal populations in African rainforests using indirect count methods under conventional distance sampling (Plumptre, 2000; Wanyama et al., 2010). Our study shows that using Bayesian inference to estimate the posterior distribution of a change in population density between two survey periods enables assigning a degree of belief that a change in density has occurred at a specific percentage (Tables 3 and 4). For example, we estimated with near certainty (0.98 probability) that the chimpanzee population density declined by at least 10% (i.e., ~75 animals; [95% CI: 66, 85]) across the study area from 2007 to 2021 for the two forest reserves combined (Table 3). Estimating the posterior distribution for a change in population density between two survey periods facilitates the detection of smaller changes in density (e.g., 5%). Our results are parallel to those of Kühl et al. (2017), who estimated a decline of 80.2% between 1990 and 2014 of the western chimpanzee (*Pan troglodytes verus*) across its range. The estimated declines were due to habitat loss, human–wildlife conflicts, diseases, poverty, and a breakdown in protected area management.

During the surveys, all anthropogenic threats (e.g., signs of logging, snares, mining) observed along transects were recorded. Thus, chimpanzee declines could be attributed to increased human activities such as cutting poles and trees, pit sawing, gold mining, and laying of snares. The 2023 chimpanzee conservation action plan for Uganda ranked habitat loss as the major threat affecting the persistence of chimpanzees across their range in the country (MTWA, 2023).

We estimated that the population density of elephants increased by 50% from 2007 to 2021 in Maramagambo (~38 individuals) with a probability of 0.99 (Table 4). A recent aerial survey of large mammals in the neighboring savanna habitat that is contiguous with Maramagambo estimated a significant increase in the local abundance of elephants between 2014 and 2018 (Lamprey et al., 2023). As such, most of the increase in population density of elephants in Maramagambo may be attributable to

TABLE 4 Realized density (mean and 95% CI), the probability of change by certain percentages of increase between 2007 and 2021, and the number of days (mean and 95% CI) that signs of elephants remained visible estimated using the modified hierarchical distance sampling model.

Site	Density		Probability of change				No. days	
	2007	2021	5%	50%	100%	150%	2007	2021
MFR	0.17 (0.13, 0.21)	0.57 (0.49, 0.66)	1	0.99	0.94	0.41	253 (188, 332)	30 (23, 38)

Abbreviation: MFR, Maramagambo Forest Reserve.

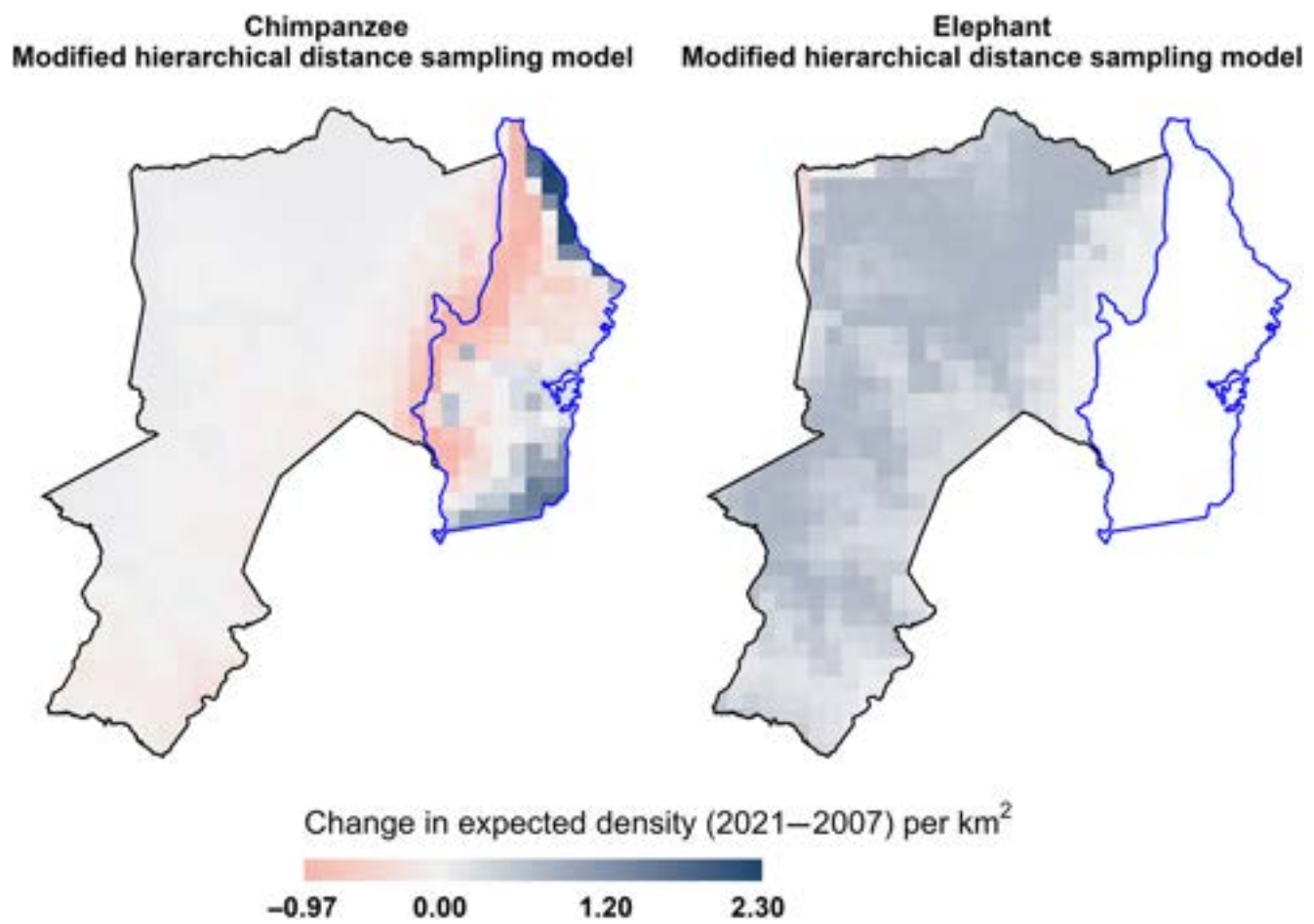


FIGURE 7 Map showing the spatial changes in expected density from 2007 to 2021 for chimpanzees and elephants. Chimpanzee estimates are shown in the Maramagambo and Kalinzu Forest Reserves, while elephant estimates are shown in the Maramagambo Forest Reserve only. The decline in chimpanzee population density was estimated to be higher in Kalinzu compared with Maramagambo, while the increase in the population density of elephants was more pronounced toward the western boundary of Maramagambo.

immigration from the savanna habitat, possibly for thermal regulation, to escape bush fires, and/or a lack of forage during the December–February dry season. A study on the distribution and abundance of elephants in Queen Elizabeth National Park revealed immigration into and emigration from the contiguous Kibale National Park during the June–August and December–March dry seasons, respectively (Buss & Savidge, 1966). Our results suggest that the aerial surveys, which usually cover open habitats like savanna, may underestimate elephant population sizes as individuals move into forests. Although it is difficult to estimate elephant densities in forested habitats, the indirect sign data suggest that Maramagambo is an important habitat for elephant populations in the landscape. Considering that African savanna elephants are endangered and have lost a substantial amount of habitat over the last century, our results provide critical information for conservation planning to further enhance and aid in their recovery.

Combining all available sign data in the modified hierarchical distance sampling model enabled the estimation of the number of days that the sign data from Visit 1 remained visible (i.e., the decay rate). Previous sign decay rate estimates obtained from field observational studies in East and West Africa forests varied between 29 and 147 days and 45 and 144 days for elephant dung and chimpanzee nests, respectively (Bessone et al., 2021; Kouakou et al., 2009; Meier et al., 2021; Nchanji & Plumptre, 2001; Plumptre & Reynolds, 1996). One of the major factors that influences the decay rates of chimpanzee nests (Bessone et al., 2021; Kouakou et al., 2009; Morgan et al., 2016) and elephant dung (Nchanji & Plumptre, 2001) is precipitation. As the frequency and intensity of precipitation increases, the sign decay rate should also increase. Generally, chimpanzee nests and elephant dung decayed faster in 2021 compared with 2007 (Tables 3 and 4). However, while chimpanzee nests decayed faster in Kalinzu (high elevation with more precipitation) than in Maramagambo (low elevation with less precipitation) in 2007, they decayed more slowly in Kalinzu than in Maramagambo in 2021. This may be because the 2021 survey was made in the December–February dry season, while the 2007 data were collected during the September–November wet season, which differentially affects decay rates in both forests. The standing crop (i.e., Visit 1 signs) sampled during the 2007 survey would have been produced during the June–August dry season, and we thus expect more nests and dung to have been visible (i.e., slower decay rates; Tables 3 and 4). Similarly, the standing crop sampled during the 2021 survey is likely to be a function of the September–November wet season, and most of the signs would have decayed (i.e., faster decay rates; Tables 3 and 4). However, similar

chimpanzee nest decay rates between Maramagambo and Kalinzu in 2021 suggest that precipitation patterns were more similar in the September–November wet season in which most of the nests observed during Visit 1 would have been produced. Regional climate models predict that the Albertine Rift will become warmer and wetter, with mean annual precipitation projected to increase by 3% by 2030 and 12% by 2090 from a 1990 baseline (Seimon & Picton Phillips, 2012). In addition, a study on the variation of rainfall patterns in western Uganda that incorporated ground measurements, remotely sensed data, and human perceptions indicated that rainy seasons were becoming wetter and the dry seasons were becoming drier across a 23-year period between 1983 and 2016 (Salerno et al., 2019). Thus, it is important to estimate survey-specific sign decay rates to enable the accurate conversion of sign density to animal density due to high variability in the sign decay rates across seasons and weather. For example, the nest decay rate of the pygmy chimpanzees (*Pan paniscus*) was found to be increasing over a 15-year period in the Congo basin as a result of decreasing precipitation, suggesting potential climate change impacts (Bessone et al., 2021).

Estimating sign decay rates using the modified hierarchical distance sampling model assumes that population density is stable over time (i.e., between Visit 1 and Visits 2–3). Due to the seasonal movement of elephants into the forest during the dry season (2021 survey), Visit 1 and Visits 2–3 dung data may have represented different subsets of the population, which would violate the assumption of a stable population across sampling visits. Thus, the estimated elephant dung decay rate for the 2021 survey (i.e., 30 [23, 38] days) may not be representative of the resident elephant population in Maramagambo (Table 4). To deliver meaningful sign decay rates, it is important that the animal populations are stable across all surveys.

Chimpanzee expected density generally increased with increasing elevation; in 2007, this relationship was estimated as unimodal with a peak between 1310 and 1380 m (82% of Kalinzu occurs at an altitude greater or equal to 1380 m), but in 2021, the relationship was estimated as monotonic (Figure 6). These different chimpanzee–elevation relationships between the two survey periods may reflect overall declines in chimpanzee density in 2021 and/or seasonal difference in habitat use. Changes in fruiting patterns have been found to influence the distribution of a chimpanzee community in Nyungwe National Park along an elevation (1744–2951 m) gradient (Green et al., 2020). For elephants, expected density generally decreased with elevation; this relationship was monotonic for both the 2007 and 2021 surveys. The differences in spatiotemporal abundance patterns of elephants in the

study area across an elevation gradient between 2007 (survey conducted in wet season) and 2021 (survey conducted in dry season) might be explained by the seasonal movement of elephants during the dry season from the savanna habitat into the forest to feed on tree foliage, access streams, and to remain in proximity to the water in Lake Edward (Eltringham, 1977). Using a static variable such as elevation that correlates with climate variables to model the abundance of species across time thus provides a window into the seasonal patterns of habitat use. Our modified hierarchical distance sampling model offers several advantages over traditional approaches to analyzing indirect count data, most notably (1) the ability to make inferences on spatial patterns of density and (2) the use of data from all visits to improve the estimation of covariate effects on density (Figure 6). Using conventional distance sampling models, we found that the precision of realized density estimates for chimpanzees and elephants varied according to the encounter rate variance estimator used in maximum likelihood implementations, and that Bayesian inference provided much more precise density estimates (Figure 4). However, studies that apply conventional distance sampling using maximum likelihood rarely report the variance estimator used. Conventional distance sampling models are widely used for indirect count studies and will likely continue to be the status quo given the availability of user-friendly software (Buckland, 2001). To facilitate a transition to Bayesian analysis, we provide the complete code for our analyses, including data formatting, model fitting, and postprocessing.

Based on our results, we suggest the following recommendations to improve the use of indirect count data for wildlife monitoring:

1. Analyze data with Bayesian inference to improve the precision of animal density estimates and to assess changes in population density over time. Bayesian inference facilitates interpretation of population changes (it is easy to compute changes in density over time with uncertainty from posterior distributions) and does not require the use of the delta method (a theorem that allows the approximation of parameter uncertainty under assumption of asymptotic distribution; Beutner, 2024) to approximate uncertainty, leading to more precise estimates.
2. When indirect count data are collected following the marked sign count approach, we recommend applying the modified hierarchical distance sampling model when making inferences about population density across space and time; conventional distance sampling may be a viable alternative when the aim is to estimate only average population density across a study area or large variations in spatial abundance patterns is not expected.
3. Incorporate Visit 1 data in the analysis of marked sign count data and include relevant covariates. Multiple (noncollinear) covariates that are hypothesized to influence the distribution and abundance of the target species can be included in the modified hierarchical distance sampling model to account for variations in patterns of abundance.
4. Consider reanalyzing historical indirect count data collected via a marked sign count approach using the modified hierarchical distance sampling model to evaluate any changes in sign decay rates across space and time in relation to climate change or other types of land use changes.

Despite the extra effort required to obtain conversion factors, indirect count methods remain critical for estimating population densities of species that are difficult to study directly. The modified hierarchical distance sampling model presented here maximizes the use of all available data collected with marked sign count protocols, thereby producing the most complete picture of cryptic populations, including spatiotemporal density and the abiotic factors that affect realized patterns of abundance. Improved methodological approaches will provide enhanced opportunities to detect changes in hard-to-study animal populations, leading to better conservation outcomes in the long run.

AUTHOR CONTRIBUTIONS

Samuel Ayebare and Elise F. Zipkin conceptualized the study and the analysis and wrote the original draft. Samuel Ayebare conducted all analyses. Neil A. Gilbert supported the analysis and contributed to writing the manuscript. Andrew J. Plumptre and Simon Nampindo collected the data and contributed to writing the manuscript. All authors reviewed and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ayebare et al., 2024a) and code (Ayebare et al., 2024b) are available from Dryad (<https://doi.org/10.5061/dryad.4j0zpc8nz>) and Zenodo (<https://doi.org/10.5281/zenodo.14199995>), respectively.

ORCID

Samuel Ayebare  <https://orcid.org/0000-0003-1215-486X>

Neil A. Gilbert  <https://orcid.org/0000-0003-0949-5612>

Andrew J. Plumptre  <https://orcid.org/0000-0002-9333-4047>

Elise F. Zipkin  <https://orcid.org/0000-0003-4155-6139>

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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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