

Monitoring spatiotemporal dynamics of large herbivores across an African rangeland using hierarchical multi-species distance sampling

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Abstract

A relative lack of standardised long-term monitoring data often limits the ability of African conservancies to quantify their efficacy to protect wildlife. In this study, we combined eight 2-km long transects surveyed monthly between October 2017 and March 2020 (total 240 transects sampled) with a hierarchical multi-species and multi-season distance sampling modelling framework to: (1) estimate monthly density of an ensemble of 10 different large herbivores and (2) understand how species respond to changes in vegetation productivity and time across the Naboisho Conservancy in the Greater Mara Ecosystem, Kenya. We documented a total of 55,298 individuals from 6830 animal groups. The median coefficient of variation for all density estimates was 27.67%. On average, number of groups was higher at intermediate levels of vegetation productivity. We found that in general, populations of large herbivores remained stable in the conservancy during the study period, except for wildebeest which decreased in density. We showed that multi-species monitoring frameworks can be used to understand how species abundance changes across space and time, providing indications as to how they are responding to environmental dynamics or management prescriptions—both of which are valuable tools for under-resourced wildlife conservancies.

KEY WORDS

abundance, hierarchical distance sampling, Maasai Mara, monitoring program, NDVI, savanna, wildlife conservancy

Résumé

Le manque relatif de données standardisées de suivi à long terme limite souvent la capacité des conservatoires africains à quantifier leur efficacité en matière de protection de la faune et de la flore. Dans cette étude, nous avons combiné huit transects de 2 km de long examinés mensuellement entre octobre 2017 et mars 2020 (240 transects échantillonnes au total) avec un cadre de modélisation hiérarchique multi-espèces et multi-saisons d'échantillonnage à distance pour: (1) estimer la densité

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mensuelle d'un ensemble de 10 grands herbivores différents et (2) comprendre comment les espèces réagissent aux changements de productivité de la végétation et au temps dans la zone de conservation de Naboisho dans l'écosystème du Grand Mara, au Kenya. Nous avons répertorié un total de 55 298 individus appartenant à 6 830 groupes d'animaux. Le coefficient médian de variation pour toutes les estimations de densité était de 27,67 %. En moyenne, le nombre de groupes était plus élevé à des niveaux intermédiaires de productivité de la végétation. Nous avons constaté qu'en général, les populations de grands herbivores sont restées stables dans le conservatoire au cours de la période d'étude, à l'exception des gnous dont la densité a diminué. Nous avons démontré que les cadres de suivi multi-espèces peuvent être utilisés pour comprendre comment l'abondance des espèces change dans l'espace et dans le temps, fournissant des indicateurs sur la façon dont elles réagissent à la dynamique environnementale ou aux prescriptions de gestion - deux outils précieux pour les conservatoires de la faune sauvage qui manquent de ressources.

1 | INTRODUCTION

Globally, populations of large herbivores are declining rapidly (Nelson, 2008; Ripple et al., 2015). These declines are particularly concerning across East Africa (Craigie et al., 2010; Ogutu et al., 2011), where large herbivores play important top-down ecological roles in savanna ecosystems. Grazing, for instance, promotes primary productivity (Frank et al., 1998; Hurnly, 1991), regulates plant diversity and stability (Ebel et al., 2022; Post, 2013), alters fire regimes by preventing build-up of senescent material (Archibald & Hempson, 2016), and maintains savanna structural and functional heterogeneity (Asner et al., 2009; Du Toit & Cumming, 1999; Porensky & Veblen, 2012). Large herbivores can also act as important seed dispersers (Albert et al., 2015) and play integral stabilising roles in ecological food webs (Dobson, 2009).

The decline of large herbivores across East Africa can be explained by human encroachment and population growth (Lamprey & Reid, 2004; Wittemyer et al., 2008), increased fencing (Jones et al., 2019; Løvschal et al., 2017), climate change and drought (Ogutu et al., 2007; Okello et al., 2016), land-use change (Ogutu et al., 2014; Waithaka, 2004), and the replacement of wildlife with their domestic counterparts (Ogutu et al., 2016). Whilst protected areas play a central role in safeguarding wildlife against these major threats, they are rarely large or connected enough to encompass the vast home ranges and migratory routes of large herbivores (Caro & Scholte, 2007; Newmark, 2008; Stabach et al., 2022). For instance, the majority of wildlife populations in Kenya occur on rangelands outside areas under formal protection (Ogutu et al., 2016; Tyrrell et al., 2020). Thus, conservation outside protected areas is critical across rangeland ecosystems (Tyrrell et al., 2020; Western et al., 2020).

The Kenyan wildlife conservancy model, which allows individuals, corporate bodies, groups, or communal landowners to designate their properties for the 'purposes of wildlife conservation and other compatible land uses' (KWCA, 2016), is becoming central to the fulfilment of conservation goals across African rangelands beyond protected areas

(Tyrrell et al., 2020; Wu et al., 2018). Currently, 177 wildlife conservancies exist in Kenya, encompassing approximately 11% of the country's land area (KWCA, 2016). In many of these conservancies, landowners receive lease payments in exchange for land-management practices previously demonstrated to be beneficial to wildlife, primarily in the form of revised livestock grazing practices (Bedelian & Ogutu, 2017). Particularly important are those wildlife conservancies established on communal and private land in a contiguous network around the Maasai Mara National Reserve, a region that attracts a high influx of tourists. Conservancies across this region were created as a direct response to declines in wildlife and were established in locations where communities were willing to participate in wildlife conservation (Wu et al., 2018). Consequently, evaluating whether conservancies are promoting positive or negative wildlife conservation outcomes relies on the ability to accurately monitor and understand complex spatiotemporal dynamics. However, obtaining unbiased and precise estimates of wildlife abundance is a challenging task, both logically and economically.

Distance sampling is an efficient and popular methodology to estimate abundance and monitor animal populations (Buckland et al., 2001; Kelt et al., 2019). The methodology addresses the problem of detection by acknowledging that animals are more difficult to see the farther they are from the transect line (Buckland et al., 2001). Accounting for imperfect detection is particularly important in conservation management to avoid incorrect parameter estimates and resulting in misleading or erroneous conclusions (Guillera-Arroita, 2017). Conventional distance sampling, however, does not incorporate spatial variation and a relatively large number of observations (60) are required to get abundance estimates (Buckland et al., 2001). More recently, density surface modelling and hierarchical distance sampling models have been developed to accommodate such variation in abundance across transects as a function of environmental covariates (Miller et al., 2013; Royle et al., 2004). These methods are vital because they provide an understanding of 'why' populations vary across a region, in addition to 'how' populations are changing. Importantly, hierarchical distance sampling modelling

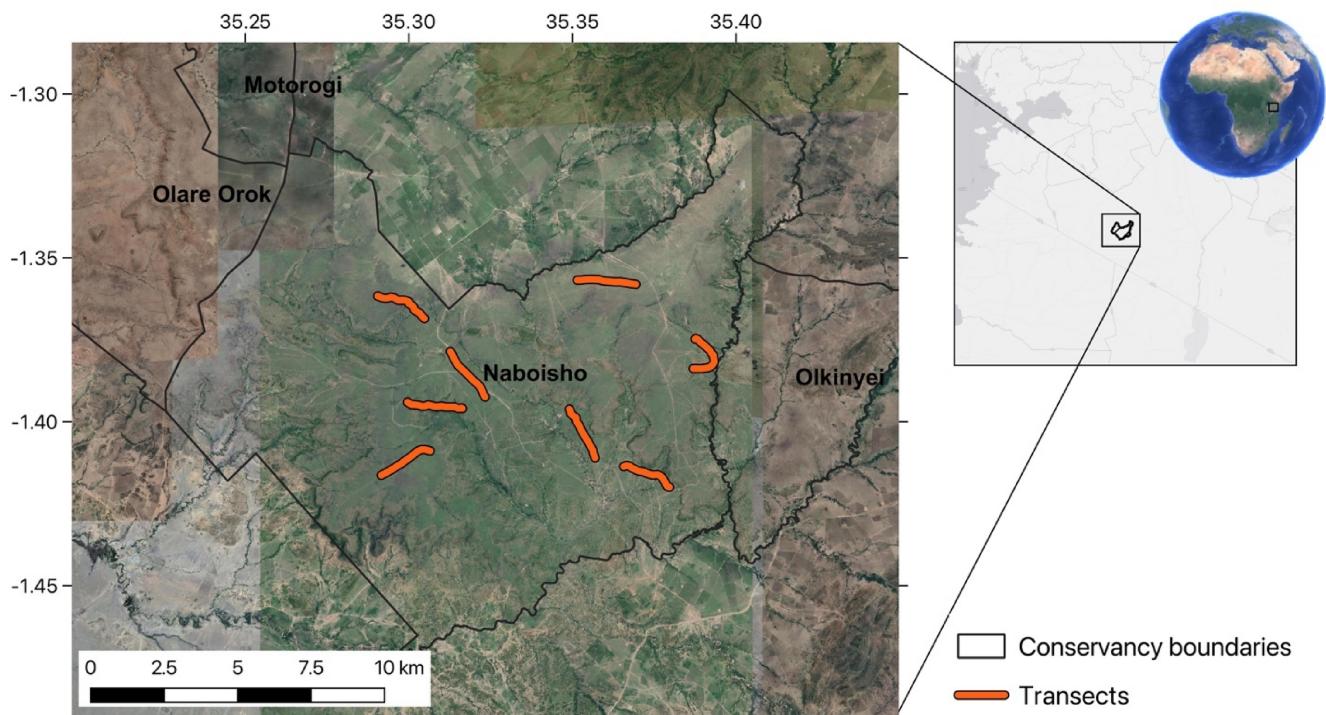


FIGURE 1 Location of Naboisho Conservancy and the eight transects used to study and monitor animal populations.

has been further expanded to integrate data from multiple species, sharing information across species while maintaining the identity of each individual species, enabling the study of rarer species with few observations (Dorazio et al., 2006; Farr et al., 2019; Sollmann et al., 2016).

In this study, we implemented a hierarchical multi-species and multi-season distance sampling modelling framework (Farr et al., 2019; Sollmann et al., 2016) to monitor the density of an assemblage of large herbivores in the Naboisho Conservancy—a wildlife conservancy located centrally in the Greater Mara Ecosystem, Kenya. Our aim was to combine a long-term dataset of line-transect surveys with a multi-species hierarchical distance sampling analysis to: (i) estimate monthly density of an ensemble of 10 different large herbivores and (ii) understand the effects of vegetation productivity and time on the number of groups of each large herbivore species and the community (i.e., increased, decreased or remained constant) across the conservancy. We present the results of the study in a Shiny App that can help managers visualise and interact with the information (<https://ramirodcrego.shinyapps.io/NaboishoSpAbu/>).

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in Naboisho Conservancy, formed in 2010 and situated between the Olare Orok, Motorogi, Ol Kinyei, and Nashulai conservancies, the Pardamat Conservation Area, and the Masai Mara National Reserve within the Greater Mara Ecosystem in

Narok County, Kenya (Figure 1). The Naboisho Conservancy covers ~200 km² and comprises more than 600 landowners. Eight wildlife tourism ventures are currently in operation throughout the conservancy, with restrictions on the number of tourists to prevent the adverse effects of high tourist numbers and associated vehicle traffic (Broekhuis, 2018).

The region is characterised by a wet period between November and May and a dry period between June and October, with rainfall peaking in November/December and March/April (Mahony et al., 2021). Severe droughts are common across the region and generally associated with fluctuations in the El Niño-Southern Oscillation, which can trigger severe reductions in vegetation productivity and high mortality of animals (Ogutu et al., 2007). The conservancy is characterised by a savannah ecosystem dominated by grass species, notably oat grass (*Themeda triandra*), rat's tail (*Sporobolus africanus*), pearl millet (*Pennisetum meyanum* syn. *Cenchrus meyanus*), and couch grass (*Cynodon dactylon*). Three species of tree predominate, whistling thorn (*Vachellia (Acacia) drepanolobium*), orange leaf croton (*Croton dichogamus*), and desert date (*Balanites aegyptiaca*). In addition, relatively high numbers of red thorn (*Vachellia (A.) gerrardii*), fever tree (*Vachellia (A.) xanthophloea*), sicklebush (*Dichrostachys cinerea*), and white raisin (*Grewia bicolor*) are encountered (Monadjem & Virani, 2016).

2.2 | Data collection

Eight 2-km long permanent transects were surveyed each month between October 2017 and March 2020 (30 months), resulting in a

total of 240 transects sampled. Transects followed established roads in the conservancy and were placed >1 km apart to maintain independence in animal counts. An effort was made to place transects on fairly straight roads. All but one of the transects followed straight lines (Figure 1). As a result, we did not expect density estimations to be biased due to the lack of linearity in the transects. Animals are habituated to the regular vehicular traffic along the road network in the conservancy. Therefore, we assumed that roads did not influence the animals' distributions. Transects were driven in the mornings at a constant speed of 10 km/h. Across the study period, a team of eight trained observers were deployed per month, with a single observer counting all individuals and groups of herbivores at each transect. Species identity, group size, linear distance to the centre of the group (using a laser rangefinder), and the angle to the centre of the group were recorded. All animals within 5 m of each other were considered part of the same group. We included 10 species of large herbivores for which we had sufficient data for analysis (i.e., >20 observations; Sollmann et al., 2016): Coke's Hartebeest (*Alcelaphus buselaphus cokii*), eland (*Tragelaphus oryx*), Masai giraffe (*Giraffa tippelskirchi*), Grant's gazelle (*Nanger granti*), impala (*Aepyceros melampus*), Thomson's gazelle (*Eudorcas thomsonii*), topi (*Damaliscus lunatus jimela*), common warthog (*Phacochoerus africanus*), common wildebeest (*Connochaetes taurinus*), and plains zebra (*Equus quagga*).

To understand the effect of vegetation productivity on the density of wild herbivores, we used the Normalised Difference Vegetation Index (NDVI). The NDVI has been shown to be a good predictor of forage quality and an important explanatory variable of abundance and habitat use of various herbivore species (Pettorelli et al., 2014; Ryan et al., 2012; Tyrrell et al., 2017). We averaged NDVI values from the 250-m Moderate Resolution Imaging Spectroradiometer (MODIS) data product (MYD13Q1) at each transect area (2×1.2 km). The MODIS NDVI product consists of 16-day composites computed from atmospherically corrected surface reflectances for which water, clouds, heavy aerosols, and cloud shadows have been masked out. We matched the time of each survey with the closest obtained MODIS imagery following Crego et al. (2021). We standardised NDVI variables to a zero mean and unit (1) standard deviation. Further, we estimated NDVI trends across the study period by estimating monthly mean and standard deviation from all MODIS pixel values across the conservancy. We fit a linear model to the average NDVI values across the 30 months of the study period to visualise the trend in NDVI.

2.3 | Distance sampling model

To monitor species densities, we adapted previously developed hierarchical multi-species multi-season distance sampling modelling frameworks (Farr et al., 2019; Sollmann et al., 2016). In our analysis, we adopted a static time approach, estimating population size N_t across months t without accounting for how changes in population size were explained across time (i.e., without directly modelling colonisation and extinction processes across transects

and between months; Kéry & Royle, 2021). We assumed population closure during the time in which transects were conducted each month. In distance sampling, abundance or density is estimated by accounting for the reduction in detectability of animal counts as a function of distance from the transect line (Buckland et al., 2001). We assumed that data were collected according to the model assumptions, such that all animal groups on the transect line were perfectly detected, animal groups did not move from their locations as a response of the approaching observers, and distances were recorded accurately (Buckland et al., 2001). For analysis, we truncated the data to 300 perpendicular metres from the transect line, discarding approximately 5% of the counts. For all species, we estimated the number of groups and group size per transect.

Following Sollmann et al. (2016) and Farr et al. (2019), we estimated species-specific detection probabilities for groups using the half-normal distribution for each species s at each transect j :

$$g(x) = \exp\left(-\frac{x^2}{2\sigma_{j,s}^2}\right)$$

where x is the perpendicular distance from the centre of each group to the transect line, and $\sigma_{j,s}$ is a scale parameter of the half-normal function at each transect and for each species. We used a log-link function to model σ as a function of body mass, assuming that larger animals are easier to detect, with γ_0 being the species-specific intercept parameter and γ_1 the parameter for the effect of standardised body mass. We obtained average body mass from (Kingdon et al., 2013).

$$\log(\sigma_s) = \gamma_0 + \gamma_1 * \text{BodyMass}_s$$

In the hierarchical distance sampling modelling structure, animal observations are grouped into perpendicular distance classes k (Royle et al., 2004). We used six 50-m distance classes between 0 and 300 m to both sides of the transect line. Detection probability $\pi_{k,t,j,s}$ for each species s , for each transect j , and for each sampling month t is estimated at each interval k as the integral of $g(x)$ across the distance classes from the start of one distance class b_k to the beginning of the next distance class $b_k + 1$, divided by the 50-m distance class width:

$$\pi_{k,t,j,s} = \frac{\int_{b_k}^{b_k+1} g(x) dx}{50}$$

The vector of the observed number of animal groups per species s , per transect j , and per month t within each distance interval, $y_{t,j,s}$, is the realisation of a multinomial process:

$$y_{t,j,s} \sim \text{Multinomial}\left(n_{t,j,s}, \pi_{t,j,s}^c\right)$$

where $n_{t,j,s}$ is the total number of animal groups observed across all distance intervals ($\sum_k y_{k,t,j,s}$), and $\pi_{t,j,s}^c$ is a vector containing the estimated probability that each animal group was observed within each distance interval ($\pi_{k,t,j,s} / \sum_k \pi_{k,t,j,s}$). The observed number of animal

groups per species, transect, and time, $n_{t,j,s}$, follows a binomial distribution based on the unknown latent total number of groups $N_{t,j,s}$:

$$n_{t,j,s} \sim \text{Binomial}(N_{t,j,s}, \pi_{t,j,s})$$

where $\pi_{t,j,s}$ is the sum of probabilities from each distance interval ($\sum_k \pi_{k,t,j,s}$).

Following Farr et al. (2019), we modelled the observed number of groups per species, transect, and time $N_{t,j,s}$ by assuming that number of groups followed a negative binomial distribution (specified as a Poisson-gamma mixture):

$$N_{t,j,s} = \text{Poisson}(\lambda_{t,j,s} * \rho N_{t,j,s})$$

where $\rho N_{t,j,s}$ is the gamma distributed random variable accounting for overdispersion.

We modelled the number of groups as a function of NDVI using a log-link function, incorporating the linear and quadratic effects. To assess changes in population across time due to other factors besides NDVI, we included a time coefficient on number of groups, specified as months from 1 to 30 minus the midpoint, 15.5, to assess population change across the months surveyed (Kéry & Royle, 2016).

$$\log(\lambda_{t,j,s}) = \alpha_0_{t,s} + \alpha_1_s * \text{NDVI}_{t,j} + \alpha_2_s * (\text{NDVI}_{t,j})^2 + \text{time}_s * (\text{month} - 15.5)$$

Here, $\alpha_0_{t,s}$ are the species-specific and time-specific intercepts, α_1 and α_2 are the species-specific linear and quadratic effects of NDVI, respectively, and time_s are the species-specific changes across time.

In the specification of the model, all species-level parameters (γ_0 intercept on detection probability, α trend coefficients for the number of groups) were treated as random effects, governed by community-level hyperparameters. For instance, we assumed that γ_0 followed a normal distribution with mean μ_{γ_0} and variance $\tau_{\gamma_0}^2$. As explained above, we also incorporated a random effect of month on the species-specific intercepts on number of groups and average group size.

We modelled monthly mean species-specific group sizes using a zero-truncated negative binomial distribution (i.e., a group contains at least one individual) to account for overdispersion in group size (also specified as a Poisson-gamma mixture).

$$Gz_i = zt \text{Poisson}(\mu Gz_s * \rho G_s)$$

Here, Gz_i is the group size observed for each species, μGz_s the estimated mean group size for each species and ρG_s is the gamma distributed random variable accounting for overdispersion. Mean group size for each species was described by using species-specific intercepts β_0 as a linear predictor with log-link function ($\log(\mu Gz_s) = \beta_0$). We did not include a species-level random effect on average group size as we did not expect group size to be related across the ensemble of species.

We calculated monthly species density by first multiplying the estimated number of groups per transect by the estimated averaged group size. We then summed the monthly total expected number of individuals across the eight transects, dividing by the total area sampled ($8 \times 2 \times 0.6 \text{ km} = 9.6 \text{ km}^2$). We calculated the

coefficient of variation to assess precision for each species and monthly estimate.

We fitted the model using a Bayesian framework in the *nimble* package version 1.0.1 (de Valpine et al., 2017, 2022) in R version 4.3.1 (R Core Team, 2022). We sampled the posterior distribution of parameters and derived quantities using three Markov chain Monte Carlo (MCMC) simulations, each run for 200,000 iterations. We discarded the first 100,000 iterations as burn-in and thinned by 100 to yield 1000 samples per chain and 3000 posterior samples in total. We used uninformative priors for all parameters. We checked the identifiability of parameters using the *MCMCvis* R package to calculate the overlap between the prior and the posterior distribution density, ensuring overlap was <0.35 (Gimenez et al., 2009). We assessed MCMC convergence by visually inspecting the posterior trace plots, inspecting effective sample sizes, and ensuring that the Gelman-Rubin statistic or potential scale reduction factor values for all parameters were <1.1 (Gelman & Rubin, 1992). We evaluated model goodness-of-fit by calculating the Bayesian *p*-value using the Freeman-Tukey statistic $(\sqrt{y} - \sqrt{E[y]})^2$, where y is the data and $E[y]$ is the expected value of y by the model specification (Sollmann et al., 2016). The Bayesian *p*-value is calculated as the proportion of times in which the difference between the simulated data and the expected values is larger (or smaller) than those of the original data. Values <0.05 or >0.95 indicate poor fit (Kéry & Royle, 2016). As an additional goodness-of-fit measure, we simulated the observed number of groups per species, transect, and sampled month, using the estimated number of groups and the estimated detection probability from each posterior sample (3000 simulated datasets). We then compared the observed number of groups with the mean number of groups estimated per species and per sampled month to further assess the ability of the model to recreate the observed data.

We evaluated posterior statistical support for the effect size of the parameters by calculating the probability of each parameter being greater or lower than zero (i.e., the proportion of positive or negative posterior samples). We also calculated 89% credible intervals as an indication of the uncertainty surrounding the estimated mean value of all parameters and density estimates (McElreath, 2020).

3 | RESULTS

We documented 55,298 individuals from 6830 animal groups across Naboisho Conservancy during the 30-month monitoring period (Table 1). We did not find evidence of a lack of fit in the model (Bayesian *p*-value = 0.77). Moreover, the model was able to recreate the observed data. The mean difference between the observed number of groups and averaged simulated number of groups was 0.02 (range: -4.681 to 6.811; Table S1).

Detection probabilities decayed with distance from the transects similarly for all species (Figure S1). Larger species presented slightly higher detectability than smaller ones [median effect: 0.03; 89% Credible Intervals (CRI): -0.02, 0.09; probability 84%]. Estimated

Species	Observed nr. Of groups	Observed nr. Of individuals	Average group size	Minimum group size	Maximum group size
Hartebeest	47	146	3.11	1	9
Eland	94	700	7.45	1	98
Giraffe	170	494	2.91	1	12
Grant's gazelle	322	1029	3.20	1	18
Impala	767	5618	7.32	1	100
Thomson's gazelle	1810	13,922	7.69	1	162
Topi	463	1313	2.84	1	35
Warthog	447	1328	2.97	1	19
Wildebeest	1928	23,557	12.22	1	250
Plains zebra	782	7191	9.20	1	193

TABLE 1 Number of observed groups, total number of observed individuals, and the average, minimum, and maximum group size for 10 species of large herbivores observed across Naboisho Conservancy, Kenya, for the period October 2017–March 2020.

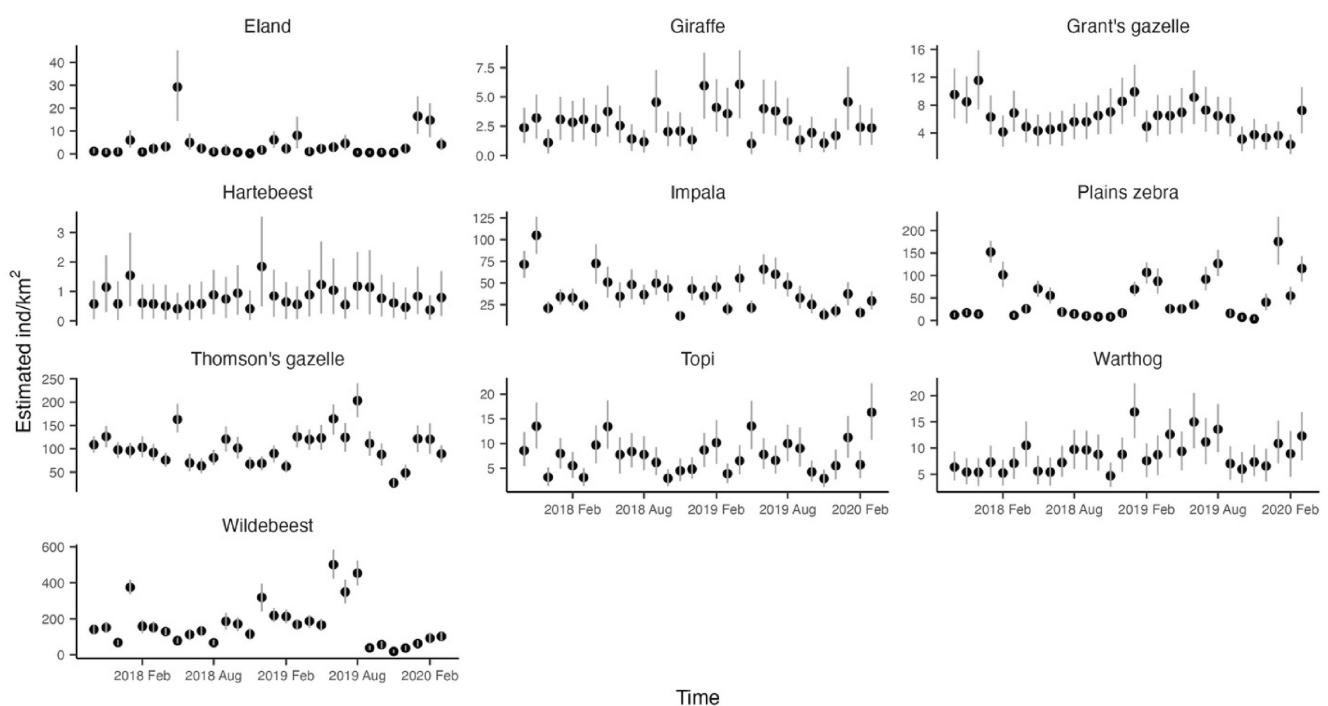


FIGURE 2 Estimated median density (dots) and 89% credible intervals (vertical bars) for 10 large herbivore species monitored across Naboisho Conservancy, Narok County, Kenya, for the period of October 2017–March 2020.

density varied greatly across species (Figure 2). Partially migratory species, such as wildebeest, plains zebra, and Thomson's gazelle, were the most abundant species, with great variability in density across time (Figure 2). The median coefficient of variation (CV) for all density estimates was 27.67%. The median CV for impala, plains zebra, Thomson's gazelle, Grant's gazelle, topi, warthog, and wildebeest was <30%. Giraffe, eland, and hartebeest had median CVs of 41.4%, 62.6%, and 65.7%, respectively (Figure S2).

At the community level, the number of groups was higher at intermediate levels of NDVI given the negative quadratic effect (NDVI: median = 0.18, 89% CRI = -0.01, 0.38, 94% probability; NDVI²: median = -0.22, 89% CRI = -0.30, -0.14, 99% probability; Figures 3 and 4). At the species level, we found that the number of groups for hartebeest, Grant's gazelle, impala, Thomson's gazelle, topi, warthog, and wildebeest, was higher at intermediate levels

of NDVI, whereas the number of groups eland, giraffe, topi, and plains zebra was higher at higher NDVI values (Figures 3 and 4). Interestingly, for wildebeest and plains zebra, the response to NDVI varied more with time, with certain months showing a flat response and other months showing a strong preference for middle NDVI values, related to the animal abundance during that month (Figure 4).

The average NDVI for the conservancy fluctuated across time but presented an overall constant trend (slope = 0.00008, p-value = 0.33; Figure 5). We found a small negative effect of time on the number of groups of the entire species assemblage (median trend: -0.0111; 89% CRI: -0.0216, 0.0003; probability: 94%). However, for most species, the effect was close to zero. Only wildebeest, Thomson's gazelle and impala presented >98% probability of a negative effect of time on the number of groups (Figure 3).

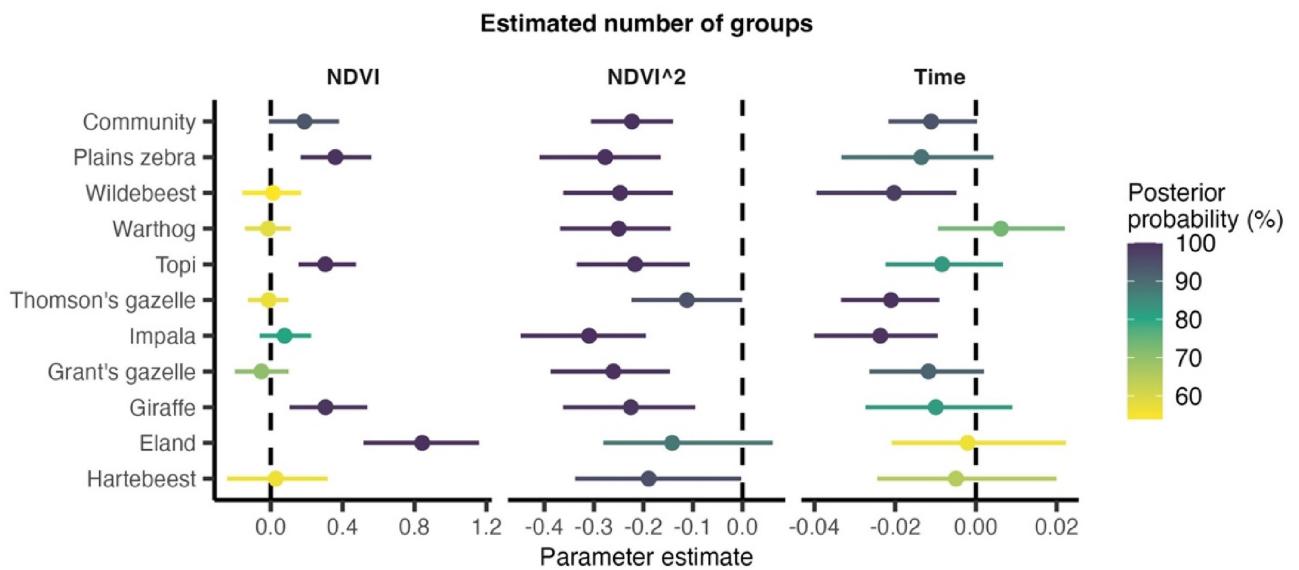


FIGURE 3 Posterior summaries of NDVI, NDVI², and time at community and species levels on the estimated number of groups for a herbivore assemblage in Naboisho Conservancy, Kenya. Dots indicate posterior medians and horizontal lines indicate 89% credible intervals. The colour gradient indicates posterior probability of parameters being higher or lower than zero.

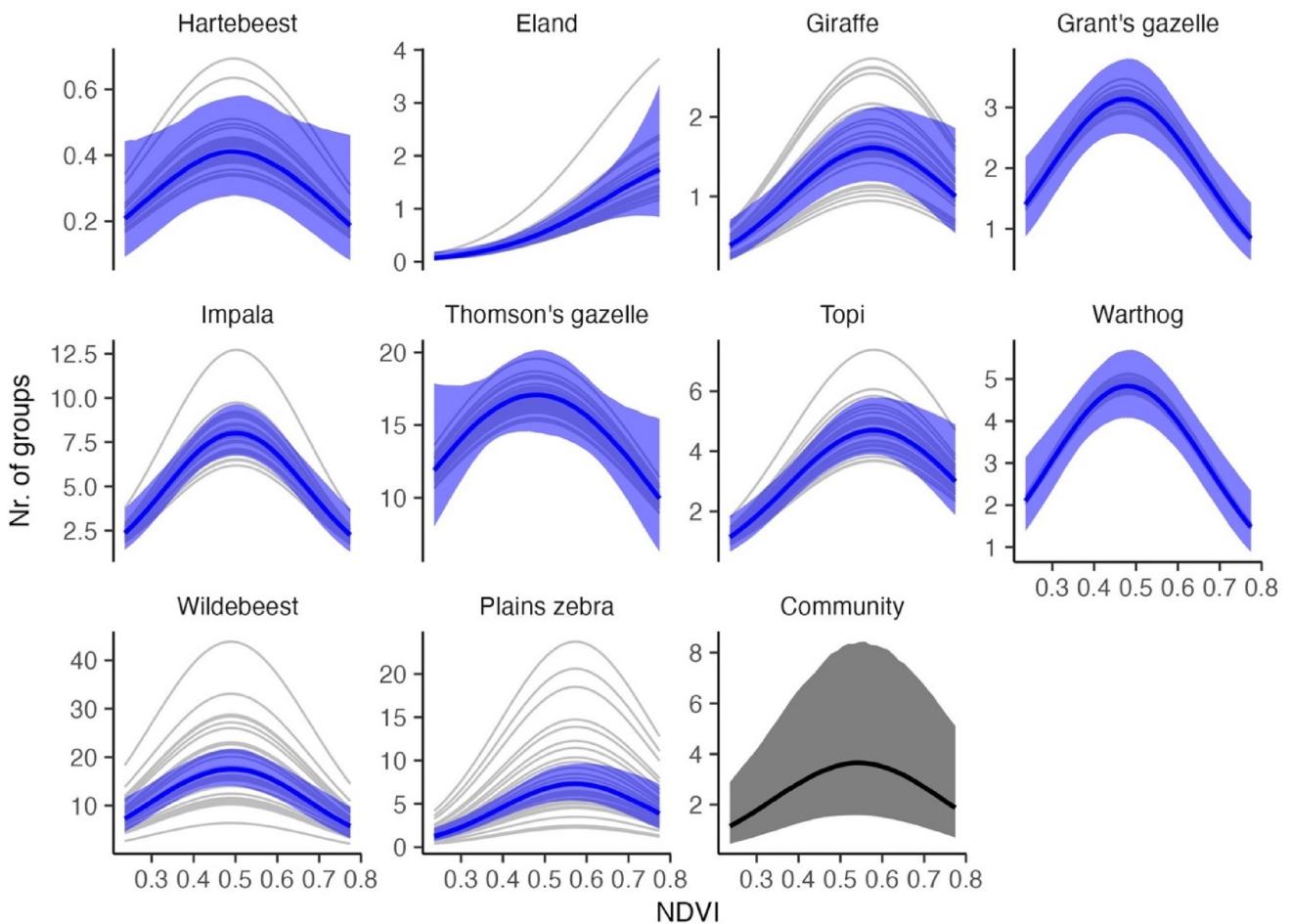


FIGURE 4 Median posterior estimated number of groups as a function of NDVI for 10 species of large herbivores across Naboisho Conservancy, Narok County, Kenya. The community response is also provided. For individual species, the blue line indicates the average estimate across all months (89% credible intervals), while the grey lines indicate each sampled month. For the community, the black line indicates the estimated median response, and the grey area indicates the 89% credible intervals.

Warthog was the only species with a positive effect, although the probability was low (74%; Figure 3).

4 | DISCUSSION

In this study, we combined systematic monthly surveys with hierarchical distance sampling methods to evaluate spatiotemporal dynamics of a large herbivore assemblage in a wildlife conservancy in the Greater Mara Ecosystem. We obtained estimates of species densities across time, corrected for detection probability, with an average $CV < 30\%$, for 7 of the 10 species monitored. For each of the total 300 density estimations, 25% presented a $CV < 20\%$, 57% $< 30\%$, and 75% $< 40\%$. As expected, CV was lower for species with more observations. Additionally, the analysis provided temporal trends in species density and spatial relationships with an index of vegetation productivity. This multi-species analysis framework is particularly valuable for wildlife conservancies, allowing them to evaluate the conservation impacts of their management actions on several species, including rare ones, by using a single analysis.

We observed high variation in density across species and time. Our results indicate that animals were generally more abundant in areas with higher NDVI, interpreted as a positive response to higher levels of vegetation productivity. In our study area, we found that higher NDVI values were linked to woody vegetation and intermediate values of NDVI were linked to grasslands (Figure S3). However, NDVI was higher in grasslands during the wet season periods (Figure S3). Thus, the higher number of groups of species at intermediate-levels of NDVI can be explained by the preferences of hartebeest, Grant's gazelle, impala, Thomson's gazelle, topi, warthog, and wildebeest species for short but nutritious grasses or forbs (Hopcraft et al., 2012; Wilmhurst et al., 1999), as well as browsing in areas with sparse woody vegetation that provides higher visibility to avoid predation (Ford et al., 2014; Hopcraft et al., 2012). The number of groups of eland, giraffe, topi, and plains zebra was higher at higher NDVI values compared to the other species (Figure 5). The increase of giraffe and eland, both of which are browsers (Kartzinel et al., 2019; Kingdon et al., 2013), is likely indicative of a preference of these species for woody vegetation. Topi and plains zebra responses to higher NDVI may be driven, however, by animals congregating in areas with abundant low-quality grasses, particularly during wet season periods (Hopcraft et al., 2012; Kingdon et al., 2013). Interestingly, we found that responses to vegetation productivity for wildebeest and plains zebras were more evident during months of higher densities, suggesting that animals congregate in the more productive patches in periods when abundance and/or competition increases.

After accounting for the effects of NDVI, we found a negative effect of time on the number of groups for several species during the study period. However, most of these effect sizes were close to zero. While we did not specifically study the drivers of species density fluctuations across time in this study, we speculate that observed variations in Naboisho Conservancy correspond with seasonal fluctuations due to migratory movements of wildebeest,

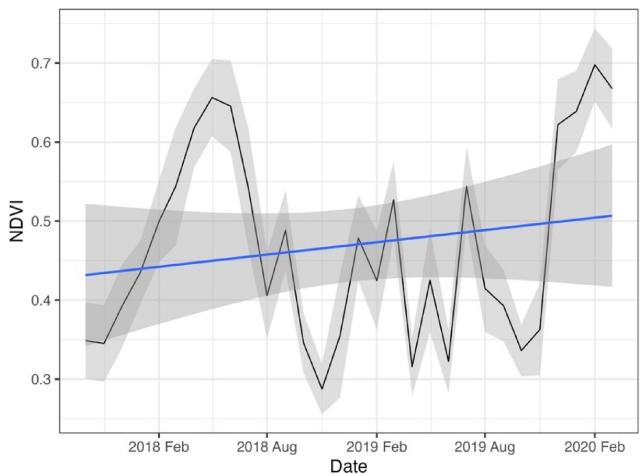


FIGURE 5 Mean + 1 standard deviation NDVI across Naboisho Conservancy between October 2017 and March 2020. The blue line represents the linear trend of mean NDVI across time + 1 standard error.

plains zebra, eland, and Thomson's gazelle populations (Bhola et al., 2012; Kingdon et al., 2013). Extreme dry periods can also explain short-term variations in species densities as abiotic factors are one of the most prevalent forces in shaping forage productivity and large herbivore abundance in Kenyan savannas (Ellis & Swift, 1988; Ogutu et al., 2007; Ogutu & Owen-Smith, 2005). The small negative effect of time on some species number of groups, such as wildebeest and Thomson's gazelles, despite the constant trend in NDVI across the conservancy could be indicative of the negative effect that increasing density of fences around the boundary of the conservancy (Løvschal et al., 2017, 2022) can have on the movement of these species (Stabach et al., 2022), with potential negative effects on populations.

Another important source of variation in animal densities is the spatial distribution of livestock across the conservancy. These data, however, were not systematically collected throughout surveys during the period of this study. The coexistence of pastoralists and large herbivores is an important consideration for wildlife conservancies across East Africa (Løvschal et al., 2019; Mwasi & Dheer, 2022; Sitters et al., 2009), but our understanding of interactions between wild herbivores, pastoralists, and their different livestock (i.e., cattle, sheep, and goat) across seasons is extremely limited (Schielz & Rubenstein, 2016). Consequently, incorporating livestock into monitoring protocols could help address this knowledge gap to improve conservancy management. This is critical given the increasing trend in livestock numbers across the region, particularly sheep and goats (Løvschal et al., 2019). It will be also important for future studies to incorporate time series analysis to further understand the reasons behind density fluctuations across seasons.

Despite the fluctuations in density and small negative effects of time on number of groups for some species, large herbivore populations appear to be stable in the conservancy. For instance, when comparing densities for the middle of the wet seasons of 2018 and 2020 (January–March), the average estimated densities for most species are

similar (Figure 6). Particularly important are topi and plains zebra, populations which have declined in Kenya over the last 40 years (Bhola et al., 2012; Kingdon et al., 2013; Ogutu et al., 2011, 2016) but appear to show signs of recovery in the conservancy. Topi median density was 5.45 ind/km² (89% CI: 2.14–10.2) for the wet season of 2018 and 11 ind/km² (89% CI: 4.17–20.3) for 2020. Plains zebra density varied largely during the wet season months of 2018 (Figure 2) with a median of 101.5 ind/km² (89% CI: 8.61–167.7), but with comparable average numbers in 2020, 114.8 ind/km² (89% CI: 43.2–208.9). Despite the negative effect of time on the number of groups for impala and Thomson's gazelle (Figure 3), average densities for the wet seasons show little difference. Impala median density was 30.6 ind/km² (89% CI: 20.0–42.5) for the wet season of 2018 and 27.8 ind/km² (89% CI: 12.0–47.3) for 2020. Thomson's gazelle median density was 96.6 ind/km² (89% CI: 78.0–119.7) for the wet season of 2018 and 109.5 ind/km² (89% CI: 78.0–149.5) for 2020. This could be due to animals gathering in larger groups, affecting number of groups but not density, calculated as number of groups times group size. Wildebeest, however, showed a marked decline in density, in line with the negative effect of time in number of groups, with median density of 169.9 ind/km² (89% CI: 126.4–338.9) for the wet season of 2018 and 86.3 ind/km² (89%

CI: 52.2–123.7) for 2020. Again, the growing number of fences in the region is negatively affecting this species (Stabach et al., 2022).

4.1 | Implications for conservancy management

Ground surveys are an economic and straightforward methodology for monitoring large herbivores in the long term when compared to other methodologies like aerial surveys, particularly for relatively small-scale areas such as community wildlife conservancies (Greene et al., 2017; Lee & Bond, 2016; Ogutu et al., 2006; Schuette et al., 2018). In this study, we integrated a long-term ground transect dataset with multi-species hierarchical distance sampling models. Implementing multispecies models allowed us to track species- and community-level metrics simultaneously, enabling us to evaluate density trends, and understand spatial responses to vegetation productivity, including less abundant species for which a single-species analysis is more difficult (Kruger et al., 2008).

Density estimates were precise, with seven out of 10 species presenting an average CV <30% for the 30 months sampled. However, for species with fewer observed groups, estimation presented low

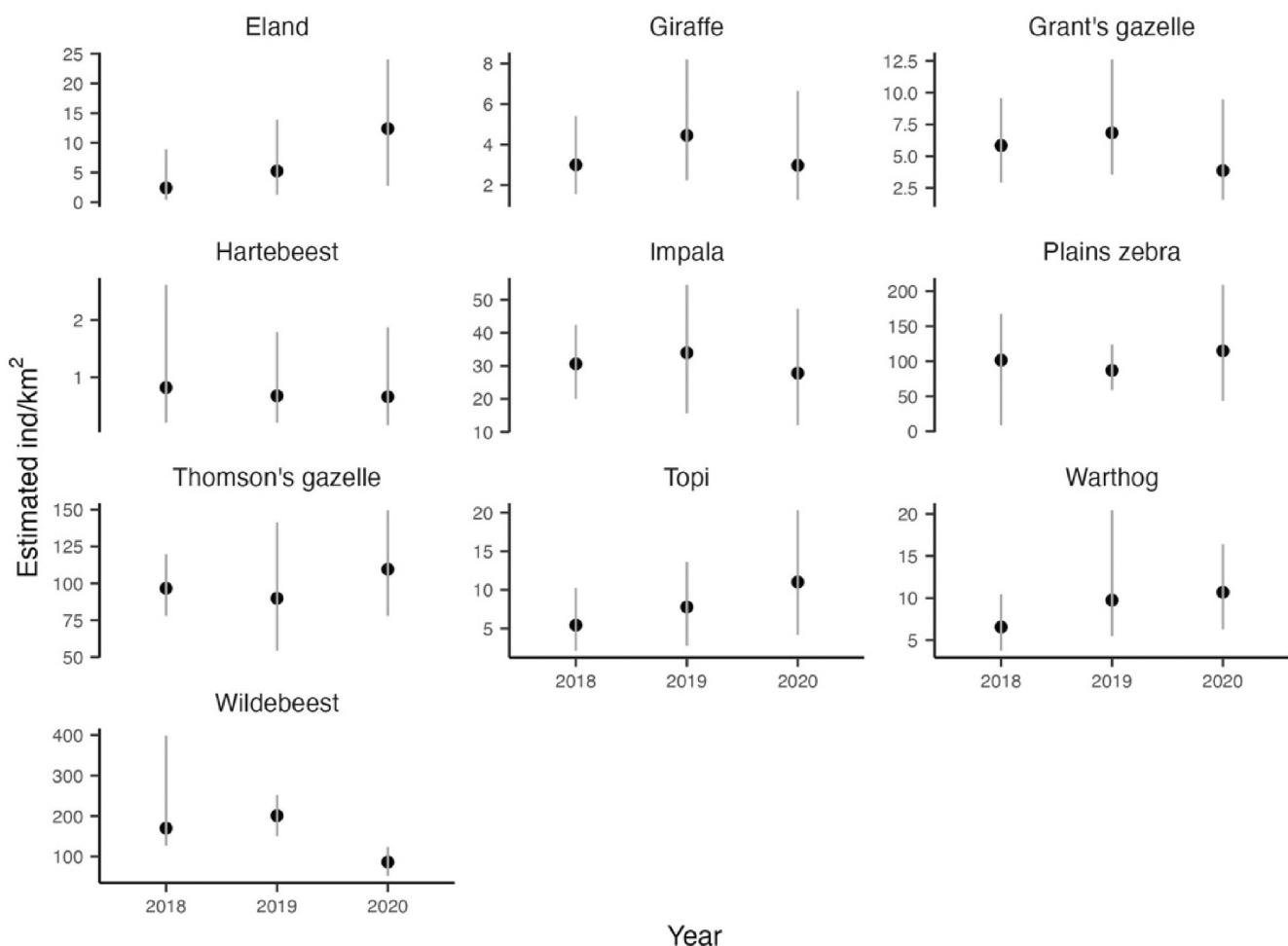


FIGURE 6 Estimated median density (dots) and 89% credible intervals (vertical bars) for 10 large herbivore species monitored across Naboisho Conservancy, Narok County, Kenya, during the middle of the wet season (January–March) of 2019, 2020, and 2021.

precision. In particular, giraffe, hartebeest, and eland presented 41.4%, 62.6%, and 65.7% CV, corresponding to the three species with the lower number of groups, 47, 94, and 170, respectively. Therefore, caution is needed when interpreting results for these species. Increasing the number of spatial replicates would help increase the number of groups observed and precision of density estimates, which in turn could also help include other rare species present in the area. Importantly, prioritising spatial replication over temporal replication can help to maximise the power to detect population trends given the same sampling effort (Andersen & Steidl, 2020).

The success of biodiversity conservation management relies, in part, on well-planned long-term monitoring programs with efficient data collection and analysis frameworks to inform decision-making processes (Lindenmayer & Likens, 2010). The framework implemented in this study serves as a model that can be replicated across other conservancies within and beyond Kenya, to monitor animal populations and understand their relationships with their environment. The Shiny App we developed (<https://ramirodcrego.shinyapps.io/NaboishoSpAbu/>) can also serve as a prototype for sharing results with stakeholders. Overall, the framework can result in valuable information for long-term monitoring of large herbivore population dynamics across networks of wildlife conservancies.

AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Study design and data collection were coordinated and performed by Stewart Thompson and Naitareu Soit. Data analysis was conducted by Ramiro D. Crego with help from Harry B. M. Wells and Grant Connette. The first draft of the manuscript was written by Ramiro D. Crego, and all authors commented and contributed to previous versions of the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The entire R code and dataset to conduct the full analysis and reproduce the results of this study are available at the following GitHub repository (<https://github.com/ramirocrego/Monitoring-spatiotemporal-dynamics-of-large-herbivores-across-Naboisho-Conservancy>) as well as a Zenodo repository (<https://doi.org/10.5281/zenodo.8418072>).

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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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