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Assessing the feasibility of density estimation methodologies for African forest elephant at large spatial scales

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ABSTRACT

Effective wildlife management requires information on population status and distribution. Survey methods that provide estimates of these population parameters can vary greatly in effort required, area covered, precision of estimates, and cost. Trade-offs are required, because increasing precision and area coverage generally requires increasing field effort and incurs a higher cost. We compare DNA- and camera trap based-spatial capture-recapture approaches (DNA-SCR and CT-SCR) to the widely-used, dung-based line transect distance sampling (LTDS) method to assess their performance when applied to three relatively large populations of forest elephant *Loxodonta cyclotis* (> 500 individuals), in order to evaluate their feasibility for future use at national and regional scales. Six of the nine surveys had a coefficient of variation below 20%; area coverage via DNA-SCR and LTDS was comparable and greatly exceeded that of the CT-SCR as applied; overall cost was highest for the LTDS surveys compared to the other two methods. We designed a new metric with which to compare survey methods: an *integrated feasibility index* (IFI). This combines three typical survey components: total area covered, level of precision achieved, and cost. The IFI suggests that DNA-SCR and LTDS are equally acceptable in terms of the combination of the three survey components, and that either survey method is suitable for large (national or regional) spatial scales for forest elephant density estimation. CT-SCR provides more precise estimates, but has double the IFI, due to the high cost per km^2. DNA-SCR in particular, given the improvements highlighted in this study, is now being used at a national scale in Gabon. In conclusion, we recommend that the use of these spatial capture-recapture (SCR) methods, and their development, continue. Future findings and improvements should be compiled across studies to ensure their robust evolution as an option for monitoring the African forest elephant across its range and inform strategies and action for its conservation.

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1. Introduction

The increasing rates of global decline of wild species' abundance and distribution is driven by the variety and complexity of threats to biodiversity (Grooten and Almond, 2018; IPBES, 2019). The key role played by biodiversity in ecosystem processes and services is becoming ever clearer, as is the need to accurately measure biodiversity in order to conserve it (Birkhofer et al., 2015; TEEB, 2010). We need efficient approaches to reliably estimate wildlife population state variables and vital rates (Williams et al., 2002) at different scales, and to understand and track their response to threats. We can then develop effective conservation actions to remediate the impact of these threats and restore ecosystem function. Across the globe, covering multiple taxa, the International Union for the Conservation of Nature (IUCN) has overseen the production of a wide variety of species conservation strategy and action plans, which are revised on a regular (often 5 or 10 year) timeline. These revisions rely on robust estimation of basic population parameters over time to enable an adaptive management approach (https://www.iucn.org/theme/species/publications/species-action-plans). Technology, survey and modeling methods for wildlife monitoring are constantly evolving, resulting in ongoing improvements in methods in species-specific monitoring programs worldwide. Such improvements, and local capacity building for their application, are a particular focus of the IUCN Species Monitoring Specialist Group (https://www.speciesmonitoring.org/), to enable best use of the data for species conservation.

Since the early 2000s, African elephants have declined dramatically: 30% and 62% in less than a decade for savanna and forest elephants respectively (Chase et al., 2016; Maisels et al., 2013). Savanna and forest elephants are subject to the same threats: poaching for ivory, habitat loss and degradation, and issues related to human-elephant conflict (CITES, 2019; Thouless et al., 2016). The steeper decline in forest elephants is particularly concerning. This genetically, ecologically, and behaviorally distinct elephant has a smaller total population size (ca. 100,000 individuals in 2013), occupies a quarter of the range, and reproduces more slowly than its savanna counterpart (Maisels et al., 2013; Thouless et al., 2016; Turkalo et al., 2018). Forest elephants are highly frugivorous (Turkalo and Barnes, 2013) and play a vital role in seed dispersal and lateral nutrient transport across large distances, shaping forest structure, and enhancing carbon sequestration (Berzaghi et al., 2019; Blake et al., 2009; Campos-Arceiz and Blake, 2011; Doughty et al., 2016; Rosin et al., 2017; Terborgh et al., 2016). Climate change appears to be reducing fruit availability, driving a decline in the fitness of elephants. For example, fruiting declined by 81% at a site in Central Gabon over the last three decades; body condition of the forest elephants at the same site declined by 11% in the final ten years of the study (Bush et al. 2020).

Because of the continuing decline in forest elephant population and range, government and nongovernmental partners launched the Great Elephant Census Forest Initiative (GEC-FI) in 2017 to assess the current status and distribution of the species across its six-country Central African range. This effort mirrors the 2014–2015 surveys across 19 countries to assess the status of African savanna elephants, (the "Great Elephant Census"). That study reported a 30% decline in that species in less than a decade (Chase et al., 2016; Schlossberg et al., 2020). The GEC-FI's main focus is Gabon, a country that is 85% forested (Verhegghen et al., 2012) and probably holds more than 50% of the remaining global population of forest elephant (Maisels et al., 2013). A second goal of the GEC-FI, and the focus of this paper, is to explore emerging or alternative methods, which might efficiently and accurately estimate population parameters of forest elephants across large forested landscapes.

The most widely used approach for estimating African forest elephant population size since the 1980s has been line transect distance sampling (LTDS) (Buckland, 2001; Buckland et al., 2015), using elephant dung counts (Alers et al., 1992; Barnes et al., 1997; Blake et al., 2008; Fay, 1991; Fay and Agnagna, 1991; Maisels et al., 2013; Thouless et al., 2016; White, 1992). LTDS has a long history of development and is well understood; a bespoke, free software for the design and analysis of surveys is available online (Distance: Thomas et al., 2010) and regularly updated. Distance sampling produces accurate estimates, accounts for potential biases in population estimation, and explicitly incorporates sources of uncertainty when designed with enough survey effort and a sufficient number of random replicates (line transects) (Buckland, 2001; Strindberg, 2012). When surveying elephants in the African forests, distance surveys on line transects necessarily depend on recording dung piles, as it is not possible to obtain records of enough directly observed elephants for a variety of reasons (Hedges et al., 2012). The conversion of dung density to elephant density relies on two multipliers (defecation rate and dung decay rate), which can result in an over- or underestimation of elephant density, unless site and time-specific estimates of each are carried out for each survey (Hedges et al., 2012): this adds to the cost and effort of each monitoring cycle. Sampling local populations of free-ranging forest elephants to adequately estimate defecation rates is challenging, because following individual elephants can be highly dangerous in forested environments (Hedges et al., 2012). Decay rate studies require locating, revisiting, and reliably classifying dung pile structure (i.e., a qualitative category applied on the basis of the degree of dung pile decay) across habitats in a spatially unbiased manner (Laing et al., 2003). When survey areas are large and access is possible only on foot (as is the case with much of Central Africa's forests, especially the protected areas within which a high proportion of the animals are found), rigorous execution of such protocols requires considerable financial and time costs, but is required to obtain accurate results (Hedges, 2012a; Hedges et al., 2012; Strindberg, 2012). Finally, Ahrestani et al. (2018) demonstrated that despite conducting carefully planned studies to obtain defecation and decay rates on a wide variety of herbivores (including elephants), there were large mismatches between abundance estimates from dung-based and sighting-based distance sampling surveys. We presume that these mismatches are caused by sampling-based overdispersion inherent in most index-based surveys (Gopalaswamy et al., 2019).

State variables (such as abundance) of an animal population may be thought of as snapshot representations of longer-term dynamics, which are described by vital rates such as survival, recruitment or movement (Williams et al., 2002). Monitoring methods based on capture-recapture theory (Amstrup et al., 2010) using individual identification (either by external

morphology or by DNA identification) dispense with the issues of the multipliers associated with dung counts. To date, population estimation of forest elephants based on individual identification has only been carried out at relatively small spatial scales. Individuals can be identified on sight (Turkalo et al., 2013b, 2018; Turkalo and Fishlock, 2015) when they visit natural forest clearings known locally as *bais* or from photographs (Head et al. 2013; Karanth et al. 2012a, 2012b). Individual identification can also use elephant DNA to assess elephant population size using capture-recapture (Eggert et al., 2003; Head et al., 2013; Hedges et al., 2013).

Spatial capture-recapture (SCR, sometimes termed SECR –spatially explicit capture-recapture) combines capture-recapture theory and spatial occurrence data from georeferenced detections to estimate abundance of a wide range of species that include big cats, birds, bears (Borchers and Efford, 2008; Efford et al., 2009; Royle et al., 2009, 2013, 2015) and elephants (Head et al. 2013). SCR data are encounters of individuals (or their DNA) where the individual, the spatial location, and the time are all known. Individual detections are assumed to be independent, and individual identity certain. The data are analyzed via likelihood or Bayesian frameworks that account for unmodeled heterogeneity in individual capture probabilities. They can incorporate covariates and class structure, and inferences can be carried out using model selection tools for likelihood-based inferences (Borchers and Efford, 2008; Burnham and Anderson, 2002; Royle et al., 2015) and for Bayesian inferences (Dey et al., 2019; Hooten and Hobbs, 2015). Over time it is possible to use SCR open population models to estimate vital rates (Gardner et al., 2018; Glennie et al., 2019). Unlike likelihood methods, Bayesian methods allow inference about latent activity centers (Royle and Young, 2008); however, the latter can be computationally heavy (Yackulic et al., 2020).

The first study using a SCR likelihood-based approach to estimate forest elephant density and home range size was carried out in a 146 km^2 area of coastal forest habitat in Gabon, in Loango National Park. A remote camera trap grid was used to photograph elephants over a 20-month period. The animals were then individually identified from facial and body features (Head et al., 2013). The long study duration raised questions about violating the assumption of demographic closure, a key assumption of SCR, and the authors advised shortening future surveys (e.g., 6–8 months) and ensuring intensive camera coverage (e.g., 60–80 cameras) (Head et al., 2013).

Molecular techniques can also be used for identifying individuals. Brand et al. (2020) used DNA-based SCR for density estimation of the species in the Gamba Industrial Complex, Gabon (900 km^2 area) using grid-structured, fixed-effort sampling for nine months, and a microsatellite DNA panel. The possibility of an unstructured sampling design, using search-encounter data with variable sampling effort (Russell et al., 2012), over large areas (Bischof et al., 2020; Elliot and Gopalaswamy, 2017) suggest that non-invasive fecal DNA sampling for SCR has potential for further development as a forest elephant population monitoring method because downtime during field sampling is minimal in such surveys. However, to ensure sound inferences on parameter estimates, it is critical to account for sampling effort by using the GPS tracks of search teams, and to understand the genotypic error rates that potentially create inaccurate matches and capture histories.

There are many benefits to employing non-invasive fecal DNA sampling for individual identification (Karanth et al., 2012a, 2012b). Animals need not be directly sighted or handled, thus avoiding any behavioral “trap response”. Biases related to sex or other individual covariates may be minor given the daily requirement for all individuals to independently deposit feces. However, fecal DNA tends to be relatively diluted and degraded; the lower quantity and quality of these samples can lead to more genotyping errors than other sources of DNA (Taberlet et al., 1996). Specifically with SCR, technical issues including allelic dropout, or PCR artefacts (false alleles or drop-in) can cause genotypic inaccuracies, which result in sample matching errors across sampling occasions: these include missed recaptures (“ghosts”) and false recaptures (“shadows”) (Creel et al., 2003; Lampa et al., 2013; Mills et al., 2018; Pompanon and Samadi, 2015). Recent advances in forest elephant genotyping with SNPs (single-nucleotide polymorphisms) that are suitable for the analyses of DNA obtained from dung offer promise, as these markers may be less prone to errors than the microsatellites used in other studies (Bourgeois et al., 2018, 2019). Because SNP markers are biallelic, more of them may be required to be able to separate individuals, although more markers may result in more genotyping errors. Another advantage of the use of SNP markers is that they can be analyzed in the laboratory in Gabon. This greatly reduces the time between sample collection in the forest and the laboratory work, and eventually this might be also true across the range of the species. In this study, we develop a panel of informative SNP markers with sufficient power to discriminate between individuals.

When deciding to use a particular method to survey a species, wildlife managers and conservation scientists need to choose from a variety of available and evolving methods, such as those described above. Indeed, since 2016 the IUCN Species Monitoring Specialist Group (https://www.speciesmonitoring.org/) has been working towards improvements in, and uptake of, survey and monitoring methods and logical choices thereof for each species in different situations across the world (Stephenson, 2018). It is difficult to apply a universal metric across various species and situations to make these decisions, because the choice of a monitoring method needs to be closely tied to the monitoring question being posed (Krebs, 1991; Nichols and Williams, 2006) in the face of limited resources. Failure to relate the monitoring question with the scale and methodology can lead to flawed scientific inferences (see Gopalaswamy et al., 2019, for a case study with tigers). Decision trees have been produced for wildlife in general (Strindberg and O’Brien, 2012) and for the great apes (Kuehl et al., 2009), based on what one wishes to know about the population. The most recent published manual for elephant surveys and monitoring covers a wide range of methods (Hedges, 2012b). It specifically includes a chapter which guides the reader to the method most suited to their requirements, based on size of the area of interest, whether absolute population size or simply occupancy is needed, whether drivers of abundance are to be identified, or demographic metrics, or trends over time, and relative costs of the various techniques. The advantages and disadvantages of each type of method are also clearly shown. However, due to their date of publication, none of these publications incorporate spatial capture-recapture methods in detail. In this study, our aim was to

explore spatial capture-recapture using both DNA and images derived from camera traps, alongside the more commonly used LTDS, in order to estimate status and distribution of forest elephant populations with at least 500 individuals. This was with the eventual aim of the possibility of future monitoring at national and regional scales. We compared estimated precision, feasibility, and cost-effectiveness of each method, across three intact forested landscapes (>1500 km^2). We also carried out the first wide-scale application of the DNA-SCR approach using a SNP marker panel for population assessment of this taxon. Our findings provided a data-driven assessment of each of the three methods, for eventual use in estimating forest elephant abundance and trends across Central Africa.

2. Methods

2.1. Study area

Our study was focused on the country of Gabon in Western Central Africa, which, in 2013, was estimated to hold about half of all African forest elephants and encompasses about a third of the current species' range (Maisels et al., 2013; Thouless et al., 2016). Forest elephants' movements in Central Africa are influenced by fruit abundance, habitat quality, the level of protection, and the degree of human pressure - in particular the presence and geometry of unprotected roads (Blake et al., 2008; Maisels et al., 2013; Vanthomme et al., 2013; White, 1994a; Yackulic et al., 2011). We selected three sites, all IUCN Category II protected areas, which comprised a range of habitats and ecological contexts relevant to forest elephant conservation (Fig. 1a).

Loango National Park (1500 km^2), created in 2002 (Government of Gabon, 2002a), lies in the Ogooué-Maritime province in southwest Gabon, and is contiguous with the Atlantic coast. The relief is a low, sandy, undulating plateau, penetrated by the Ngové Lagoon (220 km^2) which partially separates the park into eastern and western sectors. Although dominated by lowland tropical forest, the vegetation is highly diverse, with an ocean-to-inland habitat gradient starting with coastal savannas, followed by a littoral forest fringe, *Raphia* forests, papyrus-dominated areas and swamp forests along the main rivers and around a large lagoon, and finally the terra firma forests. The climate is a transitional equatorial type with a dry season lasting from late May to late September/early October. Mean annual rainfall is 1750 to 1850 mm. Mean annual temperature is 25–26 °C, dropping by 3–4 °C during the dry season (Vande weghe, 2007).

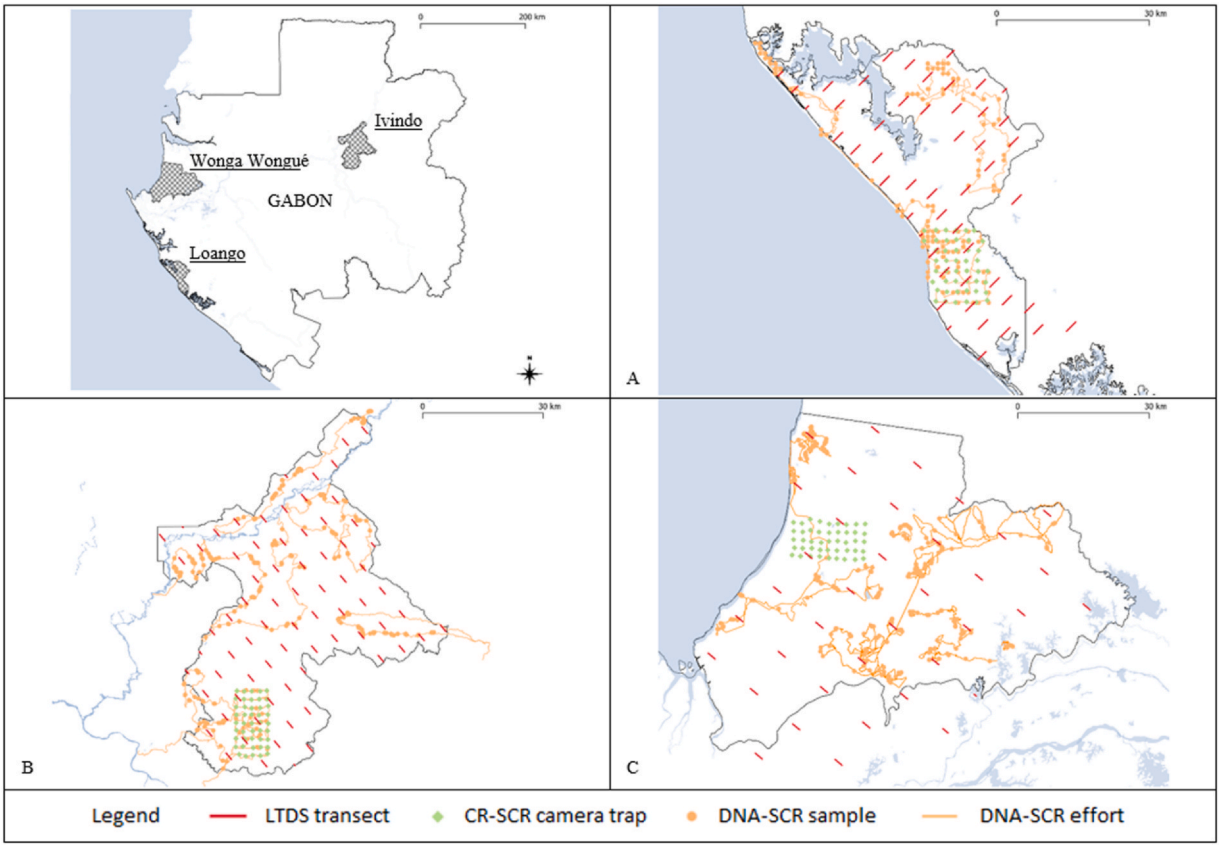

Fig. 1. Three sites: Loango National Park (A), Ivindo National Park (B), and Wonga Wongué Presidential Reserve (C), Gabon, each surveyed with three methods in parallel to determine the feasibility of each method for estimating forest elephant population density.

Ivindo National Park (3000 km^2) was also created in 2002 (Government of Gabon, 2002b). It straddles the Ogooué-Ivindo and Ogooué-Lolo provinces in central Gabon. The Ivindo River, a biogeographical barrier, cuts through the Park from northeast to southwest; its Djidji tributary runs from east to west from the center of the Park to the south. The Park includes a series of rounded plateaus (350 m) and Mount Kinguie (748 m) in the south. The "peninsula-like" north of the Park is known as the Ipassa Plateau. Ivindo NP is dominated by old-growth lowland humid forest and surrounded by logging concessions. Swamp clearings, or *bais*, dot the landscape and are highly attractive to forest elephants and other wildlife due to their mineral-rich soils. The climate is a transitional equatorial type with the main dry season from June/July to early September. Mean annual rainfall is 1750 mm and mean annual temperature is 24 °C (Momont, 2007; Vande weghe, 2009).

Wonga Wongué Presidential Reserve (4281 km^2), formerly commercially logged in the 1990s, was first declared a National Park in 1967, and then gazetted as a Presidential Reserve in 1972 (Government of Gabon, 1967, 1972). It became a RAMSAR site in 1986 (Ramsar Convention Secretariat, 2021). It lies north of the Ogooué River and is in the Estuaire, Ogooué-Maritime and Moyen Ogooué provinces in southwest Gabon, along and contiguous with the Atlantic coast. The relief is a sandy plateau rising to just under 300 m, with several (mostly inactive) canyons similar to those in the Bateké NP far to the East. It is drained to the south by tributaries of the Ogooué River, and to the north by those of the Komo River. About 70% of the Reserve is lowland forest, dominated by *Aucoumea klaineana* and *Sacoglottis gabonensis* (Wilks, 1990). As with Loango NP, the vegetation gradient starts at the west (at the Atlantic beach) through to the eastern limits roughly 60–80 km inland. Large savanna patches are found inland throughout the Reserve, embedded within the forest, the largest of which is roughly 50 × 20 km. The climate is transitional equatorial with the main dry season lasting from July to September. Mean annual rainfall is 2000 to 2400 mm. Mean annual temperature is 25–26 °C (Vande weghe, 2007).

All the sites had a similar range of human pressure (between 0 and 40 on the Human Footprint Index, which ranges between 0 and 100, where zero is least influenced by humans and 100 the most influenced; Venter et al., 2016a, 2016b). Elephant poaching for ivory has been recorded in all three sites, but in Wonga Wongué and Loango, road access is only from the eastern (inland) side compared to Ivindo, which lies a few kilometers north of the country's railway line, a few kilometers south of another national road, and its northernmost extremity lies within 10 km of the provincial capital (Makokou).

2.2. Survey methods

We surveyed forest elephants at each of the three sites. We estimated their population density using three different methods from December 2017 through to March 2019. In order to meet the population closure assumption, we attempted to complete surveys with each method in parallel within a given site, in as short a sampling period as possible. Landscape features that attract forest elephants are site-specific and include *bais* in Ivindo (Momont, 2007), savannas in Wonga Wongué (Mills et al. 2018), and papyrus swamps in Loango (Eggert et al., 2014). Seasonally abundant food sources are related to these features, such as new grass growth after savanna burning, or peak fruiting of *Sacoglottis gabonensis* (Morgan, 2009; White, 1994b). We therefore carried out our surveys in the months when populations were more likely to be closed, by avoiding seasons when local concentrations and/or long-distance movements of elephants were known to occur. Each site was completed before moving to the next site.

2.2.1. DNA- Spatial Capture-Recapture (DNA-SCR)

To obtain forest elephant individual identities for SCR modeling, we sampled dung piles across the *terra firma* of each site within a sampling area that is large enough to encompass numerous forest elephant home ranges (with a single home range defined as > 100 km^2; Blake et al., 2008; Poulsen et al., 2016) and according to an unstructured sampling design (Elliot and Gopalaswamy, 2017). To maximize our sample size, we followed paths of least resistance across a variety of habitats, which often consisted of established elephant trails leading to "hotspots" (i.e., areas that attract forest elephants), such as salines, fruiting trees, mountain ridges, river crossings, and *bais*. We sampled dung piles that we considered to be less than 24 h old, based on color, odor, and presence of recent elephant footprints. The exterior surface of the dung pile boli was gently scrubbed using an Isohelix buccal swab (Cell Projects, U.K.) (Bourgeois et al., 2019). The swab tips were immediately stored in 2-mL light-protective Eppendorf tubes containing storage buffer (Stabilizing Kits, Isohelix, Cell Projects) following the manufacturer's instructions.

We extracted DNA using the QIAamp Fast DNA Stool Mini Kit (Qiagen) and Isohelix Extraction Kit (Cell Projects, U.K.) following the protocol described in Bourgeois et al. (2019). We performed DNA extraction blanks alongside every 96 extractions in order to monitor contamination. All samples yielding an adequate quantity of forest elephant DNA (DNA concentration > 0.01 ng/μl), as determined from a species-specific quantitative PCR test targeting a small nuclear sequence of 130 base pairs, were retained for genotyping (Bourgeois et al., 2019). A subset of 15 independent nuclear DNA SNP markers (loci names CL_370, CL_708, CL_1606, CL_2068, CL_2831, CL_3824, CL_7790, CL_7859, CL_8849, CL_9831, CL_9867, CL_10251, CL_3673, CL_4367, CL_5547) was selected among a panel of 107 validated SNP genotyping assays, based on high minor allele frequency (MAF > 0.3) and assay quality, both assessed using a previous dataset of elephant genotypes from across Gabon (Bourgeois et al., 2018). In addition, an assay, amplifying small fragments of the orthologous sexual chromosome zinc finger protein genes ZFX/ZFY (65 base pairs), was used to determine sex (Bourgeois et al., 2021). All genotyping was performed using Kompetitive Allele Specific PCR (KASP) assays (LGC Genomics) on a StepOne Real-time PCR system (Applied Biosystems) in single-locus reactions, using 3 μl of 1:10 diluted DNA, 5 μl of KBIO High ROX Master mix (LGC Genomics) and 0.1 μl primer mix. Thermal cycling conditions followed manufacturer's recommendations, except that the number of PCR cycles was extended up to 43 or 52 cycles

to ensure sufficient fluorescent signal intensity and improve clustering of samples. All genotyping cluster plots were visually checked for accuracy by two independent observers and rescored manually as appropriate. Samples that failed to amplify or unambiguously cluster into one of the three distinct genotype groups were scored as missing data (no-calls). For purposes of quality control, two negative controls were included in each 48-well plate, and three samples from each plate were replicated into the next plate. The genotyping error rate was calculated as the proportion of mismatching loci within the replicates.

After the first run of the assays, all samples with more than 30% missing data, which is expected to be correlated with poor amplification (Morin et al., 2001; von Thaden et al., 2017), were discarded to reduce the risk of genotyping errors. For the remaining samples, no-calls were rerun once. We also applied a targeted multi-tubes approach in order to correct potential allelic dropout in the dataset (Frantz et al., 2003; McKelvey and Schwartz, 2005; Vallant et al., 2018). Pairs of genotypes matching at all but one or two loci were identified, and their apparent homozygous mismatching loci were rerun once to confirm the homozygous genotype or correct it as heterozygous.

We calculated the probability of identity between unrelated individuals (P_{ID}) and between siblings ($P_{ID\ SIB}$) using Genalex v6.5 (Peakall and Smouse, 2012) to estimate the required number of markers to reach a $P_{ID} < 10^{-5}$. We considered this value reasonable given the most recent estimate of Gabon's forest elephant population (ca. 50,000 individuals, Maisels et al., 2013). We also set a threshold of $P_{ID\ SIB} < 2 \times 10^{-3}$ to account for the high chance of sampling related individuals (Waits et al., 2001) due to the social structure of the species (Archie et al., 2008; Turkalo et al., 2013a). Based on these values, all consensus genotypes with zero or one missing locus were retained for the identification of individuals. Two individuals were considered matches if they presented strictly identical genotypes at all but ≤1 locus per individual where data was missing, thus ensuring a minimum of 14 identical loci within a pair of matching genotypes.

For each site, capture histories for all unique individuals on the basis of genotypic matching were compiled along with their sex and location. We considered the entire field session as a single sampling occasion and assumed population closure (i.e. that birth, death, immigration, and emigration was unlikely to occur) given the short survey period and the deliberate choice of seasons where movements were minimal. The sampled area at each of the three study sites was subdivided into 1 km x 1 km grid cells, where the centroid of each cell corresponds to a trap location for the analysis, a resolution compatible with Milleret et al. (2018). The area of integration for the SCR analysis was generated by placing a 7.5 km buffer around these trap locations at a 750 m resolution (Efford and Boulanger, 2019). Estimated detection parameters were plotted post-hoc to check that there was no truncation bias and increasing the buffer width had no discernable effect on the estimated density. We accounted for effort, measured as the natural log of meters walked per grid cell, because of an expected positive relationship between number of detections and amount of effort (Efford and Fewster, 2013; Elliot and Gopalaswamy, 2017; Russell et al., 2012). We collapsed capture histories to binary proximity detector data allowing only one detection per individual per grid cell per day, to assure independence between capture events.

We fitted full likelihood-based SCR models using the *secr* library (version 4.2.2; Efford et al., 2009) in the R programming environment (RCT 2020, R version 4.0.1) to estimate population. We treated the distribution of range centers in the population (the state model) as a homogeneous Poisson point process. Hybrid mixture models using the half-normal detection function (the observation model) were fit to the data assuming both constant and sex-specific detectability (g_0) and spatial scale (σ) for each site (Table 1). These hybrid models were developed to account for heterogeneity in detection probabilities when class covariate data for a proportion of data are known (e.g., sex) and served as the appropriate option to be used across both types of data (DNA and camera traps). However, there are uncertainties associated with the interpretation and efficiency of these parameters (Efford, 2019). Therefore, we justify the usage of these models to only recognize the presence of heterogeneity in capture probabilities due to sex differences and not for the purpose of reporting sex ratios. The model-averaged density estimates were obtained based on each model's AIC weight (Burnham and Anderson, 2002) to incorporate model uncertainty in the final density estimate. The total area surveyed was measured in km^2 and comprised the trap locations buffered by the spatial scale (σ) (as a model-averaged estimate) multiplied by the square root of 5.99 (Royle et al., 2013). It describes 95% of likely movements of all forest elephants present within the study area when the half-normal detection function is used.

2.2.2. Camera Trap Spatial Capture-Recapture (CT-SCR)

A total of 45 passive infrared camera traps (Bushnell Trophy Cam HD, protected with a metal security case) were spaced evenly throughout the trap grid (180 km^2), which was divided into 2 km x 2 km grid cells. Trap spacing was conservatively set relative to home range size, with traps spaced less than twice the spatial space parameter (Sollmann et al., 2012). We derived the 95% use area for CT-SCR in the same way as we did for DNA-SCR. The trap grid was representative of the site and included different habitat types; it was limited in size due to time and cost constraints yet similar to that of the earlier CT-SCR study

Table 1
Model set considered during SCR analyses for Loango, Ivindo, and Wonga Wongué, Gabon.

Model	Detectability (g_0)	Spatial scale (σ)	Sex ratio (r)	Description
g_0(effort), σ(.), r(sex)	*Constant*	*Constant*	*Sex*	Both g_0 and σ constant with r estimated.
g_0(effort+sex), σ(sex), r(sex)	*Sex*	*Sex*	*Sex*	g_0 and σ a function of sex with r estimated.
g_0(effort+sex), σ(.), r(sex)	*Sex*	*Constant*	*Sex*	g_0 a function of sex and σ constant with r estimated.
g_0(effort), σ(sex), r(sex)	*Constant*	*Sex*	*Sex*	g_0 constant and σ a function of sex with r estimated.
g_0(effort+sex), σ(sex), r(0.5)	*Sex*	*Sex*	*0.5*	Both g_0 and σ a function of sex assuming an even r.

Note: Detectability (g_0) and spatial scale (σ) are either modeled as constant (.) or in terms of sex (sex) with the apparent sex ratio (r) estimated (sex) or fixed at 1:1 (0.5).

(Head et al., 2013). We placed camera traps close to the center of each grid cell, usually at the intersection of forest elephant trails, to maximize the probability of detecting forest elephants. Camera traps were set on active video mode, and placed at a height of between 1.0 and 1.2 m from the ground. This was to maximize the chance of obtaining high-quality images of individual forest elephant facial features and unique markings, whilst minimizing potential damage to the cameras by elephants. At the end of each sampling period, all cameras were retrieved, videos were downloaded, backed up in duplicate, and uploaded into Timelapse2 (Greenberg and Godin, 2015) using database templates specifically developed for this project.

Videos with forest elephants were sorted into "identifiable" or "not identifiable", based on the quality of the images; the latter were discarded. The remaining images were examined by an experienced researcher familiar with a similar procedure used at *bais* (Langoue Bai, Ivindo NP) that identified individuals through a combination of unique facial and body characteristics, including notches and holes on each ear, relative size and symmetry of tusks, shape of the tail and sexual organs (Turkalo et al., 2013a; Turkalo and Fishlock, 2015). Information from each forest elephant image was recorded on an identification card. An individual was assigned a unique identification code when at least three of five unique identifiers were apparent. When examining each additional video, one researcher compared the image with any previously recognized individuals, and a match was declared if all identifiers corresponded. A second researcher reviewed the identification process and any discordance on identifiers and matches was noted and discussed with a third researcher who made a final decision.

Capture histories and SCR modeling followed the same format described in the DNA-based methods, with the exception of subdividing the survey into multiple sampling occasions of one day each, with associated binary effort (i.e., a grid cell with functional camera in the entire 24-hour period or not).

2.2.3. Line Transect Distance Sampling (LTDS)

We designed, implemented, and analyzed distance sampling surveys (Buckland, 2001) along line transects using the Distance software (Thomas et al., 2010) and following the guidelines outlined in Hedges et al. (2012) and Strindberg (2012). Expected sampling effort (i.e., aggregate number of km walked along transect lines) varied by site: 128 km, 150 km and 61 km for Loango, Ivindo, and Wonga Wongué, respectively. Determining the total amount of sampling effort requires a trade-off between survey precision and cost. Precision, as reflected by the percent coefficient of variation (CV), was expected to be < 20%, with the predicted number of dung detections > 200, on the basis of parameters derived from three previous site-specific studies (i.e., encounter rates between 4 and 6 dung piles per km and dispersion parameters between 3 and 5) (Maisels et al., 2010; Motsaba and Aba'a, 2012; WCS, unpublished data). We designed transect lengths that could be completed in a single day (i.e., 2.0–2.5 km), with slightly longer transects at sites where there was a more open understory. Transects were orientated perpendicular to the principal drainage system, to potentially improve precision by aligning the transect parallel to expected density gradients, and placed systematically with a random start point across the entire area surveyed. Transects intersecting the edge of the study area were truncated.

We followed the standard field protocol for elephant dung surveys, including recording perpendicular distances to the center of each dung pile and assignment of stage classes (S1–S5; Hedges et al., 2012). LTDS assumes that detections are independent, dung piles on the transect line are detected with certainty, and perpendicular distances are measured accurately (Buckland, 2001; Hedges et al., 2012). Data was entered electronically using SMART-ER (Ecological Records) software (smartconservationtools.org) on a rugged smartphone (CT5 Juniper Systems) and in notebooks as a backup. Half-normal, hazard-rate, and uniform key functions with different adjustments terms (cosine, simple polynomial, hermite polynomial) were fit with 3%, 5%, and 10% right truncation of the data to improve the fit of the detection function. Model selection occurred on the basis of AIC values and the results of goodness-of-fit tests.

Defecation and dung decay rates were used to convert dung density estimates to elephant density estimates (Buckland, 2001; Strindberg, 2012). Rather than conduct defecation rate studies, which are necessary for unbiased estimation of density but potentially dangerous to execute in practice, we approximated daily defecation rates for each site using the rainfall curve of Theuerkauf and Gula (2010) and note that these rates and their respective variances may differ from those we might obtain from on-ground surveys. The precipitation data in each case was from the closest airport in the 12 months prior to the end of the survey (Port-Gentil for Loango and Wonga Wongué and Makokou for Ivindo, from the World Weather Information Service https://worldweather.wmo.int).

We conducted time- and site-specific dung decay studies using the 'retrospective' method (Laing et al., 2003). We estimated dung persistence by locating and tagging fresh dung piles before the survey and revisiting the same dung-piles at mid-survey, assigning the same stage classes used during the survey. In Ivindo, the dung located and revisited was part of a broader dung decay study by Duke University. A reasonable percentage of remaining dung must remain visible at the end of the experiment to reliably calculate the decay rate using binomial regression (Hedges et al., 2012). Dung stage class cut-off was set *post-hoc*, so that all dung categorized as decayed was excluded from analysis. We fit Generalized Additive Models with different link functions (logit, probit, complementary log-log, and cauchit link) to the binomial data (0 = decayed, 1 = visible) (Venables and Ripley, 2013). We attempted to include at least 60 dung piles per site from a range of locations across each study area, to adequately represent each site's mean dung decay rate. We used a mid-survey dung check to measure inter-observer reliability in assigning stage classes via a test submitted to all observers; which was verified for accordance using Fleiss' Kappa index (Fleiss, 1971).

2.3. Feasibility assessment

One of the main objectives of this comparative study was to aid wildlife managers and conservation scientists in choosing a reliable and informative method for large-scale monitoring of forest elephants. For this, we assembled an eight-person Technical Advisory Group (TAG) comprising experts in elephant ecology, statistics, and wildlife management. Together, we pinpointed knowledge gaps, management needs, study goals, and considered which assessment methods to test. After designing surveys, implementing field sampling, and producing preliminary results for three sites using three different assessment methods, we then worked with the TAG to discuss the inherent assumptions, potential biases, and sources of error of each method. We also discussed each method's advantages versus limitations in the context of future largescale application for estimating the size of forest elephant populations across Gabon and the Central African region.

Plans for 'scaling up' require better understanding of various logistical and technical factors involved within the context of resource and skill limitations. We examined the performance of each method by examining three indicators and combining them into an overall measure, which we term the Integrated Feasibility Index (IFI). This index uses (i) the precision of the density estimate at a given site (expressed as the estimate CV), (ii) the total area surveyed for each method, in km^2 (the study area for LTDS, or extent of the 95% use area for the two types of SCR) and (iii) the total financial cost for each method (the sum of the costs required for equipment, field staff salaries and benefits, field operations, and data processing and analysis in USD, Table A1).

We then evaluated three interactions of these indicators for each of the survey methods at each site. These interactions were: (i) representativity (CV per area surveyed expressed in $/km^2$), (ii) scalability (cost per area surveyed in USD/km^2), and (iii) cost-effectiveness (CV multiplied by the total cost in USD).

Finally, we combined the three indicators (precision, area surveyed and cost, per method), into the single IFI metric as follows: (CV x cost) / area surveyed. The IFI thus combines the three indicators in a way that provides for practical decisions on which method to use for surveys and monitoring. We calculated the mean IFI per method for each of the three study sites. Low values indicated low cost, high precision, or both when surveying large areas. We were unable to directly compare the accuracy of the density estimates among methods because the true population size at each site was unknown, and simulation exercises were outside the scope of this study. However, to gain insight on the possible bias intrinsic to each method, we examined the width of confidence intervals for the density estimates using each method, and its consistency across the three study sites, and then compared this result between the three methods.

3. Results

We completed the surveys using the three methods in a single field session in Loango (December 2017 to March 2018) and Ivindo (April 2018 to July 2018), and two sessions in Wonga Wongué (September to November 2018 for LTDS and CT-SCR and April to May 2019 for DNA-SCR). The longest survey duration was for the LTDS in Ivindo (105 days plus dung decay starting 70 days before the survey). The shortest survey was the DNA-SCR in Wonga Wongué (17 days). We collected fresh dung samples and high quality images of forest elephants at all sites, resulting in sufficient individual identifications for SCR analysis (Table 2).

3.1. DNA-Spatial Capture-Recapture

Fecal DNA sampling covered 1948 grid cells (1 km^2 each) totaling 2762 km walked (509 km in Loango, 1241 km in Ivindo, 1012 in Wonga Wongué, combined average = 10 km/day/team). We collected 394, 526, and 653 dung samples with an encounter rate of 0.8, 0.4, and 0.7 dung piles per km in Loango, Ivindo, and Wonga Wongué, respectively, over a combined 152 days in the field (track available in Fig. 1b–d).

After discarding 598 low quality samples (inadequate DNA quantity and more than 30% missing data), we generated 975 consensus genotypes with ≤1 missing locus (Table 2). We determined sex for all but 1 genotype. Genotyping error rate for all sites combined was 5.2%. After initial PCR, 14.2% of the data was considered missing (no-calls) and re-run once. Homozygous genotypes from near-matching pairs of samples (9.1%) were also re-run once to confirm or correct their scores according to our targeted multi-tubes approach (8.3% corrected as heterozygous).

P_{ID} ranged from 5.8×10^{-7} to 5.9×10^{-6} and $P_{ID\ SIB}$ ranged from 5.7×10^{-4} to 1.9×10^{-3} across the sites (Table A2), which provided sufficient power to discriminate unique individuals. We identified 251, 197, and 303 unique individuals in Loango, Ivindo and Wonga Wongué, respectively. After collapsing data for binary proximity detectors, we retained a total of 840 captures; recapture rates were 10.0%, 7.6%, and 16.2% for Loango, Ivindo, and Wonga Wongué, respectively (Table 2).

Hybrid mixture models fit to the data using the half-normal detection function where an apparent sex ratio is estimated had the highest model weights (Table 2). The model-averaged density estimate (D) was 1.59 (0.43 SE) forest elephants per km^2 in Loango, 0.49 (0.20 SE) in Ivindo, and 0.80 (0.13 SE) in Wonga Wongué (Table 2). When these models included a sex covariate, the estimated spatial scale (σ) and detectability (g_0) was larger for female forest elephants than for males at all sites (Table 2). The observed sex ratio was biased towards females, with 1:2.7, 1:2.1 and 1:2.4 for Loango, Ivindo and Wonga Wongue, respectively.

The SCR models used for the DNA-SCR surveys are approximations of those used for conventional trap arrays. Hence, dimensions are very high (approximating 1 km x 1 km grid cells to trap locations), especially when combined with a large number of individuals (fairly typical of such elephant datasets). This problem limits the analytical options available for analysis

Table 2
DNA and camera trap survey details for three sites (Loango, Ivindo and Wonga Wongué) in Gabon and spatial capture recapture model-averaged results.

Method	Site	Survey duration (days)	Person-days	Effort	Collected Samples	Quality step 1	Quality step 2	Non. Ind.Det.	Ind.Det.	Individuals (nbr, F=M|U)	Recaptures (%)	g_0 (F=M)	σ (F=M)	Elephant density (per km^2)	95% Confidence Interval
DNA-SCR	Loango	58	212	509	394	337	302	296	276	251 (184|67|0)	10.0	0.003|0.002 (0.0008|0.0010)	2245|2073 (250|372)	1.59 (0.43 SE)	0.94–2.66
	Ivindo	77	401	1241	526	323	265	248	212	197 (133|63|1)	7.6	0.001|0.001 (0.0004|0.0008)	3966|2348 (597|1012)	0.49 (0.20 SE)	0.23–1.05
	Wonga Wongue	17	400	1012	653	561	441	431	352	303 (213|90|0)	16.2	0.007|0.006 (0.001|0.002)	1567|1429 (139|218)	0.80 (0.13 SE)	0.58–1.09
CT-SCR	Loango	54	334	1778	1665	746	NA	NA	232	161 (89|65|7)	44.1	0.006|0.002 (0.001|0.001)	1794|3871 (176|548)	0.96 (0.11 SE)	0.76–1.21
	Ivindo	66	195	1960	579	470	NA	NA	121	91 (48|33|10)	33.0	0.003|0.003 (0.001|0.001)	1931|1740 (274|294)	0.84 (0.16 SE)	0.59–1.22
	Wonga Wongue	63	222	1648	929	573	NA	NA	216	148 (75|55|18)	45.9	0.005|0.006 (0.001|0.001)	2310|2266 (199|197)	0.82 (0.10 SE)	0.64–1.00

Method = DNA-based spatial capture recapture (DNA-SCR) and Cameratrap-based spatial capture recapture (CT-SCR)
Effort = km walked for DNA-SCR and camera days for CT-SCR; Collected samples = nbr of dung samples for DNA-SCR and elephant images for CT-SCR
Quality 1 = number of samples with adequate DNA quantity and quality for DNA-SCR and nbr of identifiable elephant images for CT-SCR
Quality 2 = number of samples with < 30% missing data for DNA-SCR; none for CT-SCR
Non.Ind.Det. = Non-independent detections = sum of all samples providing individual ID
Ind.Det. = Independent detections = removed data representing the same individual on the same day in the same detector (grid for DNA-SCR and camera trap for CT-SCR)
Individuals = number of identified individuals, and numbers of females, males and unassigned (F|M|U)
g_0 = detectability; F | M = estimates are shown for females and males, when sex was included as a covariate;
σ = spatial scale in km; D = elephant density; SE = standard error; CI = 95% confidence interval

and some inferences. For example, we found that Bayesian SCR models (in which activity centers are not integrated out of the likelihood, Elliot and Gopalaswamy 2017) are computationally very demanding and time consuming unless several computational strategies are applied (Turek et al., 2021).

3.2. Camera Trap-Spatial Capture-Recapture

We set 45 camera traps at each site for 54 sampling occasions (one day per occasion) in Loango, 66 in Ivindo, and 63 in Wonga Wongué, totaling 5386 camera days (Table 2). We recorded 10,196 videos, of which about a third (3173) captured forest elephants (31%): average capture rate was 0.59 elephants per camera day. 1789 videos were initially scored as identifiable; 569 of these (32%) contained sufficient characteristics to be assigned a final identity. We identified 161 individual elephants (71 recaptures, 44.1% recapture rate) in Loango, 91 elephants (30 recaptures, 33.0% recapture rate) in Ivindo, and 148 elephants (68 recaptures, 45.9% recapture rate) in Wonga Wongué. Recaptures were almost four times higher for CT-SCR (41% recapture rate, 7 SE) compared to DNA-SCR (11.2% recapture rate, 4.4 SE). We were able to assign sex to 212 females and 153 males; sex was uncertain for 35 individuals. The observed sex ratio was biased towards females but less so than for DNA-SCR, with 1:1.4, 1:1.5 and 1:1.4 for Loango, Ivindo and Wonga Wongue, respectively.

The model-averaged density estimate (D) was 0.96 (0.11 SE) forest elephants per km^2 in Loango, 0.84 (0.16 SE) in Ivindo, and 0.82 (0.10 SE) in Wonga Wongué (Table 2). More females than males were detected in all sites.

3.3. Line Transect Distance Sampling

To measure dung decay rate per site, we tagged 61 fresh dung piles in Loango, 86 in Ivindo, and 88 in Wonga Wongué. We revisited each once, between 3 and 122 days from its tag date. Two dung piles were not relocated. By the time of the revisit, the majority of dung piles were classed as S4 in Loango and Wonga Wongué (n = 48 and 61, respectively) and S5 in Ivindo (n = 54).

We classified dung in classes S1 through S3 as visible, and those in classes S4 and S5 as decayed for all three sites, resulting in a visible to decayed ratio of 80:20, 37:63, 30:70 for Loango, Ivindo and Wonga Wongué, respectively. We selected the highest AIC ranking model for Loango and Ivindo (complementary log-log and cauchit link, respectively) and model-averaged for Wonga Wongué, given the considerable variation in mean persistence time of dung at this site. Dung decay rate (i.e., mean persistence time of dung) was 46.06 days (SE 2.54; CV 5.52%) in Loango, 55.43 days (SE 7.30; CV 13.17%) in Ivindo, and 23.27 days (SE 6.06; CV 4.12%) in Wonga Wongué (Table 3). We checked inter-observer reliability in classifying dung stages by asking 11 observers to independently class 13 dung piles across the 5 stages. A Kappa value of 0.62 showed substantial agreement amongst observers.

We estimated defecation rate at the time of our study to be 18.57 dung/day (SE 1.27) in Loango, 17.92 dung/day (SE 1.38) in Ivindo, and 17.23 dung/day (SE 1.09) in Wonga Wongué (with 12-month precipitation values of 2315 mm, 2045 mm, 1783 mm, respectively). These fall between the values reported by the two defecation studies of forest elephants in Cameroon (15.9 and 19.8 dung/day in Nchanji et al. 2008 and Tchamba 1992, respectively).

Sampling effort in Loango was 93 km (46 transects in the 1819 km^2 surveyed), 131 km in Ivindo (73 transects in the 2972 km^2 surveyed) and 61 km in Wonga Wongué (35 transects in the 4895 km^2 surveyed). Transect length averaged 1.9 km (range: 0.3–2.5 km); 15 transects situated in deep water or swamps were not completed. Encounter rate was highest in Wonga Wongué with 15 dung piles/km walked (95% CI 11–20; n = 908 dung piles), followed by Ivindo with 7.9 dung piles/km (95% CI 6.8–9; n = 1031 dung piles), and Loango with 6.2 dung piles/km (95% CI 5.0–7.7; n = 580 dung piles) before right truncation of the data to improve the fit of the detection function. The final detection function used a 3% right truncation distance and a uniform key function (cosine adjustment) for Loango and Ivindo, while a 5% right truncation with a hazard rate key function (no adjustment terms) was used for Wonga Wongué. When explored in Distance, all datasets were consistent with an assumption of certain detection of dung piles on and near the line and an assumption of accurate perpendicular distance measurements. Forest elephant density was 0.86 (0.13 SE), 1.19 (0.20 SE), and 0.69 (0.22 SE) elephants per km^2 for Loango, Ivindo, and Wonga Wongué, respectively (Table 3), calculated using the two multipliers of rainfall-based defecation rate and the time and site-specific decay rate reported above.

3.4. Feasibility assessment

The best performance for each site, for each indicator and each interaction between indicators, is shown in bold in Table 4. The lower values represent the more desirable results for precision and cost (for example, for Loango, the lowest CV was obtained using the CT-SCR method, and the lowest total cost was with the DNA-SCR method). Conversely, higher values are more desirable for Area (in other words, again for Loango, the largest area surveyed was with the LTDS method). Finally, the lower the IFI, the better the method performed at the site(s) for the combination of precision and cost-effectiveness for the area.

For each method, the three interactions between the three indicators, and the IFI itself, revealed specific patterns that were not evident when the indicators were examined independently. CT-SCR was the most cost-effective of the methods as it provided the best precision –cost index (mean CV x cost = 6772 USD ± 1219 SE), but it was only used in our work for small study areas and had limited scalability. LTDS provided the best precision given the area covered (mean CV/area = 0.7 CV/km^2 ± 0.1 SE), but its cost-effectiveness was almost the same as the DNA-SCR method and both were three times less cost-effective than CT-SCR (mean CV*cost was just under $7000 for the latter). DNA-SCR was the most scalable (mean cost/area = 23.5

Table 3
Line transect distance sampling (LTDS) result for three sites (Loango, Ivindo and Wonga Wongué) in Gabon.

Method	Site	Survey duration (days)	Decay survey duration (days)	Sampling Effort (km)	Person-days	Detected dung	Visible dung	Dung decay (days)	Effectively sampled half-width (m)	Dung density (/ km^2)	Elephant density (/ km^2)	95% Confidence Interval
LTDS	Loango	81	54	93	800	580	509	46.06 (2.54 SE)	3.70	760 (93 SE)	0.86 (0.13 SE)	0.64–1.15
	Ivindo	175	122	131	1072	1031	923	55.43 (7.3 SE)	2.82	1181 (980 SE)	1.19 (0.20 SE)	0.86–1.65
	Wonga Wongué	74	37	61	462	908	883	23.27 (6.06 SE)	4.42	275 (69 SE)	0.69 (0.22 SE)	0.37–1.26

Table 4
Feasibility inputs and indices for the three surveys methods in Loango, Ivindo and Wonga Wongué.

Method	Site	CV (%)	Area (km^2)	Cost (USD)	CV/ Area*100 (/km^2)	Cost/Area (USD/km^2)	CV*Cost (USD)	IFI (CV*Cost/Area)	Mean IFI (per method)
DNA-SCR	Loango	27%	1583	**$55200**	1.7	**$34.86**	$14904	9.4	
	Ivindo	41%	**5554**	$65000	0.7	**$12**	$26650	**4.8**	**6.0 (1.7 SE)**
	Wonga Wongué	16%	2500	$60000	**0.6**	$24	$9600	**3.8**	
CT-SCR	Loango	**11%**	417	$63700	2.6	$153	**$7007**	16.8	
	Ivindo	19%	741	**$47000**	2.6	$63	**$8930**	12.1	13.8 (1.5 SE)
	Wonga Wongué	**12%**	352	**$36500**	3.4	$104	**$4380**	12.4	
LTDS	Loango	13%	**1819**	$105000	**0.7**	$58	$13650	**7.5**	
	Ivindo	**16%**	2972	$122500	**0.5**	$41	$19600	6.6	6.1 (0.9 SE)
	Wonga Wongué	37%	**4895**	$59100	0.7	**$12**	$21276	4.3	

Note: The best performance for each site for each index is shown in bold. The smaller the IFI, the better the indicated performance.

USD/km^2 ± 6.7 SE), but less precise than LTDS in two of the three sites. The IFI highlights that both DNA-SCR and LTDS have similar overall feasibility (6.0 ± 1.7 SE) and (6.1 ± 0.9 SE) respectively) while the area limitations of CT-SCR became clear (13.8 ± 1.5 SE). Wonga Wongué DNA-SCR had the lowest IFI among all sites and methods (3.8).

4. Discussion

We estimated forest elephant population density using three different survey methods in parallel in three forest landscapes in Gabon. The sites included different vegetation types (littoral forests, closed canopy swamp and terra firma forests, and savanna-forest mosaics) and area (1500–5000 km^2). The methods were DNA-SCR, CT-SCR, and LTDS. We devised a quantitative metric, the IFI, by which these (and potentially any other) methods can be compared for the best combination of precision, cost-effectiveness, and appropriateness to different spatial scales, thus facilitating future decisions as to which choice of method to use in differing situations.

Both DNA- and CT-SCR were shown to be feasible alternatives to LTDS for identifying forest elephants and estimating their population size at a given site. However, the three methods varied greatly in the amount of effort required, surface area covered, precision of density estimates, consistency of performance across sites, and cost. Trade-offs are apparent in these measures, because increasing precision and area coverage requires increasing field effort and incurs a higher cost. The DNA-SCR method (using the new SNP panel developed within this study) was a viable alternative to LTDS at one site (Wonga Wongué): it had the lowest IFI among the six site-specific methods that had a precision equal to or better than that originally targeted (CV < 20%). Deciding which method to use in future surveys will benefit from considering the findings and recommendations of this study, including examining the results of the IFI, the functional form of the IFI in relation to management objectives, along with other contextual information and any specific management requirements. For example, at specific sites, management may be keen to understand other state variables, such as sex ratios, or population dynamic parameters such as survival and recruitment. These requirements may also play a crucial role in decision-making beyond the IFI.

4.1. Detections and sample size

Collection of fresh dung using an unstructured sampling design, and image capture with a stationary camera trap grid each provided a large number of detections of individual forest elephants within fewer than three months (range: 17–77 days per site), but with a low recapture rate in some instances. Limiting sample duration was important to meet the methods' assumption of population closure, and to test the efficiency of SCR methods versus LTDS. The authors of the two previous SCR surveys on African forest elephants recognized that their studies violated this assumption, as their sampling periods were 20 months (Head et al., 2013) and nine months (Brand et al., 2020). The recapture rate for DNA-SCR in two of our three study sites was 10% or less. This was lower than in the other African DNA-SCR study (17%) in Brand et al. (2020); lower than in the Asian elephant study (21%) in Hedges et al. (2013) and also lower than in the CT-SCR method in this study. Comparing DNA-SCR with CT-SCR suggests that additional sampling using DNA-SCR may increase the recapture rate, and the precision of the density estimate. A number of recaptures were discarded because we chose to collapse data for binary proximity detectors (Table 2) in DNA-SCR to achieve spatial and temporal independence in captures at a resolution of 1 km^2 and 24 h at each grid cell, which may not have been done in other DNA-SCR studies reported above. Higher recapture rates were achieved when we deployed multiple teams simultaneously in Wonga Wongué over a wider area than at the other two sites. This tactic could be incorporated in future studies to improve DNA-SCR performance. In addition, we can consider decreasing the resolution of grid cells while still obtaining spatial independence or combining the partial binary approach (Goswami et al., 2019; Milleret et al., 2018) within grid cells at predetermined segment lengths and accumulate spatially independent dung samples, which in both cases may help increase sample size.

DNA sampling in Ivindo involved the greatest effort (401 km across 5554 km^2) of the three sites, but yielded the lowest fresh dung encounter rate (0.4 dung piles per km walked) and the highest number of low quantity and quality DNA samples that had to be discarded (53% of the original sample total) resulting in the lowest number of individuals identified (197 individuals) and a low recapture rate (7.6%). These particularities to Ivindo were not known a priori, despite a previous optimization study conducted at national scale (Bourgeois et al., 2019), and thus difficult to incorporate in the sampling design, but could be considered for any future application of DNA-SCR. 39% of samples were discarded in Ivindo after the DNA quantification step compared to less than 15% at the other two sites (Table 2). Varying extraction success across locations and seasons has been reported before in this species (Bourgeois et al., 2019). A cursory review of our sampling protocol and relationships between amplification success and sample date, location, visible condition of dung, field team members and how long they had received training, storage and transport time, and laboratory treatment revealed no clear pattern. Examining causes of low DNA amplification success in Ivindo samples, such as dietary or other inhibitors inherent to the samples could be explored to increase the sample size and presumably improve the recapture rate. Optimization of laboratory protocols such as the addition of a purification step, host DNA enrichment or whole-genome amplification techniques (Chiou and Bergey, 2018; Costa et al., 2017; Fuentes-Pardo and Ruzzante, 2017) prior to PCR have been proposed to help increase genotyping success. However, adding extra lab steps to salvage the lowest quality samples is costly and may also lead to a decrease in the quality of the dataset due to degraded DNA. Therefore, a careful assessment of genotyping errors following these additional laboratory steps is crucial to determine if they really are beneficial, compared to increasing field effort and number of samples collected. While a pilot study is essential to choose and optimize field protocols, a risk of variation of the extraction success due to unpredictable environmental factors persists, especially for a large-scale study. The availability of an in-country laboratory for determining DNA quantity per sample in near real time at the beginning of a survey or an initial pilot study at the site, plus continual monitoring of fresh dung encounter rate could help adjust field effort accordingly, increase sample size and presumably the recapture rate.

4.2. Area coverage and effort

Area coverage by the DNA-SCR and LTDS methods were comparable, and greatly exceeded that of the CT-SCR as applied. The unstructured sampling design and requirement of fresh dung for DNA-SCR meant that at the study's onset, an undetermined amount of effort was required to obtain sufficient samples. In all cases, this was achieved with less field effort than the LTDS, but the systematic transect placement of the LTDS meant that a larger area was covered in two of the three sites that was assured by design a priori. CT-SCR was confined to an approximate 200 km^2 trap grid, which meant that its area of inference was much smaller than for the other two methods, limiting its comparative usefulness for large landscapes. Increasing the distance between cameras could allow an increase in coverage area but potentially to the detriment of recapture rates and precision (Sun et al., 2014). Alternatively, constructing multiple grids or transposing a single grid repeatedly over time would result in greater area coverage with presumably similar precision. The ability of camera trapping to identify individuals, its high sample size and acceptable recapture rate, consistently high precision and low CV all suggest that exploring grid expansion is worthwhile, with the caveat that such expansion will increase costs even if camera traps are reused. This is because of the logistical effort required for deployment. It will also increase the complexity of identifying matches because there are likely to be more individuals present in the larger study area. Images from camera traps can also be used to assess body condition of elephants, providing an additional tool for monitoring of population health (Bush et al., 2020). As is normal for all camera trap and line transect surveys, multiple species were detected. For example, chimpanzee, gorilla, giant pangolin, and spotted hyena were detected by the cameras, and African forest buffalo, red river hog, and African grey parrot by the line transect work. These additional species data potentially have value for future analyses, which is not possible with DNA-SCR as applied.

4.3. Density, precision, and its consistency across sites

Elephant density estimates across the nine studies (three methods, three sites) varied within sites, but the confidence intervals of all estimates overlapped (Fig. 2). No method gave consistently lower or higher estimates across sites, therefore, obvious systematic bias was not evident.

Similarly, there was no pattern of better or worse precision for any of the three methods. Six of the nine surveys had CVs below the original target level of 20%. The three with poorer precision were the LTDS survey in Wonga Wongué, and the DNA-SCR surveys in Loango and Ivindo. Precision thus does not discount any one method; if we increased effort within the same surface areas (more camera traps/ longer or more line transects/ more fresh dung collected), there would be more detections (and presumably higher recapture rates in the DNA-SCR method), and the precision of each estimate would improve. DNA-SCR in Wonga Wongué serves as a proof of concept that this method can rapidly (17 days) achieve adequate precision (CV < 20%) at a low cost (i.e., a cost similar to the other two DNA-SCR applications). It resulted in a high sample size (653 total samples and only 34% discarded due to an inadequate quantity of DNA) and an acceptable recapture rate (16.2%). Precision could have been better in the LTDS survey in Wonga Wongué if there had been more transects and a higher sampling effort (and the cost would have been higher; more like that of the other two LTDS surveys). In LTDS, the relationship between better precision and increased effort is not linear, but rather follows the law of diminishing returns (equation 7.6 on page 243, Buckland 2001), so survey design always has to balance improved predicted precision with the increasingly costly effect of adding survey effort.

Our best forest elephant density estimates for the three sites (CV lower than 20%; large area surveyed) are 0.86 (0.13 SE) for Loango and 1.19 (0.20 SE) for Ivindo, both using LTDS, and 0.80 (0.13 SE) for Wonga Wongué using DNA-SCR (Tables 3 and 4).

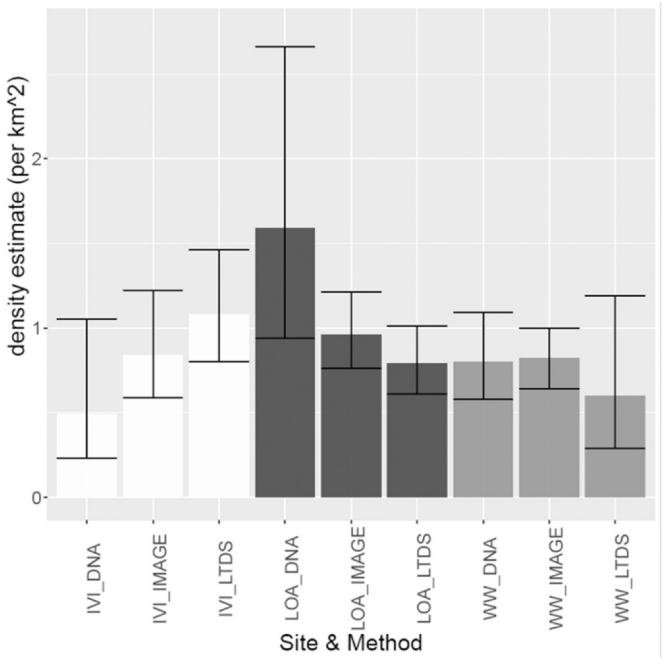

Fig. 2. Boxplot of forest elephant density estimate (/km^2) with error bars showing 95% confidence intervals for the three methods (DNA-SCR, CT-SCR and LTDS) at each site (IVI: Ivindo NP, LOA: Loango NP and Wonga Wongué PR). The variation in density estimates (/km^2) per site was considerable and many confidence intervals overlapped.

Using a combination of multiple survey methods, instead of relying on a single method to assess populations, can improve inference (Gopalaswamy et al., 2012; Nuñez et al., 2019). For example, using the inverse-weighting approach (Hartung et al., 2011), assuming that the uncertainties around maximum likelihood estimates are normally distributed and that the density was homogenous across the methods, we get a combined estimate of 0.94 (0.08 SE), 0.84 (0.11 SE) and 0.80 (0.08 SE) in Loango, Ivindo and Wonga Wongué respectively. There are gains in precision of the estimates at each site, however these gains in precision are only relevant if we assume that each method is inherently reliable in that the quality of density estimation with each method improves when sample sizes are increased.

Both SCR methods and LTDS have primary sources of error not accounted for in their estimation of density as modeled, namely error associated with individual identification (in SCR) and with the multipliers (in LTDS). The two multipliers in the latter are defecation rate and dung decay rate, and are critical for LTDS to be able to produce accurate estimations of elephant density, as they are used to convert dung density to animal density. Uncertainty introduced by these multipliers in LTDS was not easily quantifiable. Many forest elephant surveys have not determined site-specific dung decay and defecation rates due to financial and logistical constraints (Thouless et al. 2016), although modern elephant survey guidelines advise that these additional costs, especially studies to estimate decay rate, should really be included in the budget (Hedges et al., 2012; Hedges and Lawson, 2006). In our study, measuring a dung decay rate representative of the wide range of microhabitats within each site proved challenging. Fieldwork tended to produce geographically clustered dung piles that produced values of uncertain accuracy. We did not attempt to directly measure defecation rates as explained above; therefore, the values derived from Theuerkauf and Gula's (2010) rainfall curve were also of uncertain robustness.

Imperfect and qualitative classification of dung stage may also introduce inaccuracy and/or bias in dung density estimation (Hedges et al., 2012), though we mitigated this through extensive training; our mid-survey observer test (Kappa index) indicated that inconsistent classification did not appreciably impact results.

On balance, the sources of error of SCR may be easier to deal with than those of LTDS. SCR assumes that individuals are correctly identified, but in practice CT- and DNA-based individual identification is not perfect. For CT-SCR, 82% of the elephant images could not be identified to individual level. An alternative approach which takes into account spatial correlation in counts of photographed animals could be carried out: Chandler and Royle (2013), if the camera trap approach inherently fails to capture a large proportion of identifiable individuals.

Genotyping error rate with our streamlined SNP panel was around 5% with the laboratory protocols employed, including operator cross-checking to minimize process-related error and limiting panel size. Similar or higher error rates were reported with SNP markers in other studies using fecal DNA samples (Blåhed et al., 2019; von Thaden et al., 2017, 2020). In addition, we discarded low quality samples that were expected to be more error-prone, and used targeted multi-tube runs to reduce genotyping errors. Therefore we assume that our sample handling and the laboratory protocols minimized error as much as possible, given the low quantity of template DNA in fecal samples available for large-scale, non-invasive sampling. Additional

multi-tube runs for a selection of samples below a predetermined quality threshold may still decrease genotyping errors, while limiting the economic burden of conventional multi-tubes approaches that require numerous repetitions. However, given that genotyping errors cannot be completely eliminated, the strict matching, as used here, may have lowered the recapture rate if genotype errors resulted in two samples from the same individual appearing to come from different animals. Therefore, examining error-tolerant matching approaches (e.g., Sethi et al., 2016; Wang, 2016) in the future may be worthwhile in order to increase the final number of samples included in the analyses and reduce the impact of genotyping errors on individual identification, if these models prove to be accurate with small SNP panels and robust to variations of DNA quantity within non-invasive datasets. An alternative approach is the Genotype Spatial Partial Identity Model (SPIM), which uses the spatial location where the sample was collected to address genotype uncertainty in capture-recapture (Augustine and Fuller, 2020). However, this model assumes the distribution of genotypes are independent across individuals, which is not the case for forest elephants which move in highly related groups (Schuttler et al., 2014; Turkalo and Barnes, 2013).

4.4. Costs and integrated feasibility index

Overall cost was highest for the LTDS surveys compared to the other two methods. However, LTDS requires little post-field processing, whereas as both SCR methods require considerable image or DNA processing, and the duration and expense associated with these services will vary by technique, institution and/or country. Increasing precision for the three studies where CV > 20% (one of the LTDS and two of the DNA-SCR surveys) would increase costs as explained above. Aside from these caveats, the DNA-SCR application was most consistently economical on a per km^2 basis. The presence of the existing in-country laboratory, and the development of a streamlined SNP panel were major assets in increasing the cost-efficiency of DNA-SCR for our study. The cost of genotyping per sample was inexpensive (14 USD for a panel of 16 assays excluding extraction and labor costs) and efficiency could be further improved with the use of multiplex technologies targeting multiple sequences at once in a single reaction. These improvements may also be driven by other interests related to the DNA samples collected, including geographic origin of seized elephant ivory, or information on population structure and relatedness. In addition, the forest elephant-specific tools used here were previously developed to increase cost-efficiency in fecal datasets (Bourgeois et al. 2019); such optimization is almost certainly required for other taxa to ensure cost-effectiveness of large-scale DNA-SCR.

The IFI combined measures of precision, area covered, and cost in a single metric. This is the first time that such an index has been designed, and is an independent way to judge trade-offs between these three indicators of method performance. SCR-DNA in Wonga Wongué balanced these trade-offs well, estimating what is likely to be close to the true abundance of forest elephants at this site with good precision, with the work being both scalable and cost-effective at half the cost of what would be needed to achieve a similar CV with LTDS. Overall, mean IFI for DNA-SCR and LTDS were comparable; in terms of feasibility, both are suitable for estimating population size at large spatial scales. In contrast, the CT-SCR applications had a high IFI due to the high cost per km^2 and they are much less scalable as currently designed. It is important to notice that results from this application of IFI should not be generalized to other studies in which the relative benefits of using each method may depend in a non-linear way on study area, species and methods. Nevertheless, we have highlighted here what are the issues with each of these methods in this specific context, in the hope that our feasibility assessment framework, more than the study-specific conclusions, can be useful to guide future studies.

4.5. Conservation implications and conclusions

Determining species status, either in response to conservation measures or as an early warning of population declines, relies on robust population parameter estimation and trend analysis. Most African forest elephant surveys to date used LTDS, despite known challenges with the method's two unavoidable multipliers – defecation and decay rate – that are either difficult and dangerous, or costly and fraught with reliability issues, respectively, to obtain in a survey-specific manner. Our multi-site study examined the feasibility and performance of two uses of SCR in parallel with LTDS, and demonstrates the usefulness and potential of SCR as a feasible monitoring option for forest elephants. As an emerging approach, SCR builds on the theory of conventional capture-recapture already used for forest elephants in Asia and Africa (e.g., Eggert et al., 2003, 2014; Hedges et al., 2013) and a wide variety of other species worldwide (e.g., Dawson and Efford, 2009; Efford and Fewster, 2013; Gardner et al., 2010; Romairone et al., 2018).

Our study more thoroughly examines SCR for repeated large-scale use for forest elephant population assessment (following the smaller scale studies by Head et al. (2013) and Brand et al. (2020), both carried out within or next to our Loango study site). CT-SCR used for forest elephants could benefit from sampling designs that expand the coverage area; automated video processing to filter out the approximately 70% of videos lacking the target species would greatly streamline processing time (Whytock et al., 2020).

A design module which could identify target sample size and effort for a specified target CV based on previous or assumed fresh dung encounter rate and amplification success would improve the use of DNA-SCR for this taxon, as would techniques to reduce genotyping error, improve amplification, and account for potential errors in the identification of individuals. Exploring the quality of estimation of each method through simulation exercises and sensitivity tests may also illuminate where improvements could occur. In conclusion, we recommend that the use of these SCR methods, and their development, continue. DNA-SCR in particular, given the improvements highlighted in this study, is now being used at a national scale in Gabon. Future findings and improvements should be compiled across studies to ensure their robust evolution as an option for monitoring the African forest elephant across its range, and inform strategies and action for its conservation.

Impact statement

Data-driven comparison of three survey methods to monitor forest elephants *Loxodonta cyclotis* at large spatial scales at three sites in Gabon.

CRediT authorship contribution statement

K.S. Gobush, G. Abitsi, J.M. Fay, L.J.T. White, F. Maisels, E.J. Stokes: Conceived the project and secured funding. **A. Laguardia, K.S. Gobush, S. Bourgeois, S. Strindberg, G. Abitsi, F. Ebouta, A.M. Gopalaswamy, F. Maisels, R. Ogden, L.J.T. White, E.J. Stokes:** Designed the methodology. **A. Laguardia, F. Maisels, S. Bourgeois, F. Ebouta:** Trained staff in the methods. **A. Laguardia, F. Ebouta:** Supervised implementation and data collection. **S. Bourgeois:** Selected the panel of SNPs, Supervised laboratory work. **A. Laguardia, S. Bourgeois, S. Strindberg, F. Ebouta, F. Maisels:** Analysed the data. **A. Laguardia, K.S. Gobush:** Led the writing of the manuscript. All authors contributed significantly to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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ANNEX A

See Tables A1 and A2.

Table A1
Total financial cost for each method calculated as the sum of the costs required for equipment, field staff salaries and benefits, field operations, and data processing and analysis in USD.

Activity	Loango	Ivindo	Wonga Wongue
CT-SCR			
Equipment	$ 27,391	$ 18,800	$ 18,615
Field staff	$ 19,110	$ 18,800	$ 7665
Field operations	$ 16,562	$ 8930	$ 7665
Data processing	$ 637	$ 470	$ 2555
Total	**$ 63,700**	**$ 47,000**	**$ 36,500**
DNA-SCR			
Equipment	$ 19,320	$ 21,450	$ 29,400
Field staff	$ 17,112	$ 18,850	$ 15,600
Field operations	$ 10,488	$ 16,900	$ 11,400
Data processing	$ 8280	$ 7800	$ 4200
Total	**$ 55,200**	**$ 65,000**	**$ 60,600**
LTDS			
Equipment	$ 18,900	$ 19,600	$ 18,912
Field staff	$ 43,050	$ 56,350	$ 20,094
Field operations	$ 38,850	$ 42,875	$ 15,957
Data processing	$ 4200	$ 3675	$ 4137
Total	**$ 105,000**	**$ 122,500**	**$ 59,100**

Table A2
Probability of identity between unrelated individuals (P_{ID}) and between siblings ($P_{ID\ SIB}$) for each site.

	Probability of identity (P_{ID})		Probability of identity between siblings ($P_{ID\ SIB}$)	
Field site	At 14 loci	At 16 loci	At 14 loci	At 16 loci
Loango NP	3.90E-06	6.05E-07	1.52E-03	5.73E-04
Ivindo NP	3.58E-06	5.80E-07	1.47E-03	5.72E-04
Wonga Wongué PR	5.91E-06	1.02E-06	1.91E-03	7.70E-04

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