

Using the Formozov–Malyshev–Pereleshin formula to convert mammal spoor counts into density estimates for long-term community-level monitoring

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Abstract

Finding an appropriate method to monitor a wide range of mammal species simultaneously is notoriously difficult, as each method has its limitations. Here, we examine a formula, known as the Formozov–Malyshev–Pereleshin (FMP), which uses mean daily travel distances (day ranges) to convert spoor counts into density estimates. Availability of accurate estimates of day ranges is a limitation of the FMP formula. Here, we used allometry to estimate day ranges for those species that lacked empirical movement data and general additive models (GAM) to assess trends in density estimates. With this approach, we derived density estimates for 10 mammal species, regardless of whether they were abundant, or rare and elusive (e.g. carnivores). General additive models suggest that six species are stable or increasing, and four declining, although all nonsignificantly. Use of allometric estimates in lieu of empirical estimates led to falsely increased precision in density estimates, highlighting the need to fill the knowledge gap in movement ecology for certain species. Simulations were used to examine error introduced into trend estimates by this bias. We conclude that the FMP formula, when properly employed, can be an efficient method for simultaneous monitoring of multispecies in different functional groups.

Résumé

Il est particulièrement difficile de trouver une méthode appropriée pour surveiller simultanément une large gamme d'espèces de mammifères, car chaque méthode a ses limitations. Ici, nous examinons une formule connue sous le nom de Formozov–Malyshev–Pereleshin (FMP), qui utilise des distances de déplacement quotidiennes (écart de jours) pour convertir le nombre de traces en estimation de densité. La disponibilité des estimations précises d'écart de jours est une limitation de la formule FMP. Ici, nous avons utilisé l'allométrie pour évaluer les écarts de jours des espèces pour lesquelles il manquait des mouvements de données empiriques et des modèles additifs généraux (MAG) pour évaluer les tendances des estimations de densité. Avec cette approche, nous avons calculé des estimations de densité pour 10 espèces de mammifères, qu'elles soient abondantes ou rares et insaisissables (par exemple, des carnivores). Les modèles MAG suggèrent que six espèces sont stables ou en augmentation et quatre en baisse, bien que toutes de façon non significatives. L'utilisation

d'estimations allométriques à la place d'estimations empiriques a donné lieu à une précision faussement accrue des estimations de densité, soulignant la nécessité de combler le manque de connaissances dans le mouvement écologique pour certaines espèces. Des simulations ont été utilisées pour examiner l'erreur introduite dans les estimations de tendance par ce biais. Nous concluons que la formule FMP, lorsqu'elle est correctement utilisée, peut être une méthode efficace pour la surveillance simultanée de plusieurs espèces dans différents groupes fonctionnels.

KEYWORDS

movement ecology, Namibia, population density, Salambala Conservancy, wildlife monitoring, wildlife survey

1 | INTRODUCTION

Namibia is a leader in community based natural resource management (CBNRM) with about 20% of its total surface area allocated to communal conservancies (NACSO, 2016). Through conservancies, local communities have been empowered to benefit legally from the sustainable utilisation of natural resources directly and indirectly (NACSO, 2016). To manage wildlife sustainably, communities are obliged to conduct annual population assessments in collaboration with supporting institutions such as the Ministry of Environment and Tourism (MET) (NACSO, 2016). Community assessments of wildlife abundance and trends provide knowledge to stakeholders (e.g. wildlife managers, scientists, community members) about, for example, the effect(s) of management actions (e.g. yearly hunting quotas), wildlife responses to environmental changes (Ogutu & Owen-Smith, 2003) or the effectiveness of monitoring schemes to adequately detect trends within a constituency (Danielsen, Burgess, & Balmford, 2005; Hausser, Tagand, Vimercati, Mermod, & Fischer, 2016). Thus, conducting monitoring and evaluation of wildlife trends provide insight concerning both management decisions and resource status.

Currently, distance sampling is employed to monitor wildlife populations in Namibian communal conservancies (NACSO, 2017). While distance sampling can produce robust density estimates, the method may not be suitable for species with small body size, cryptic coloration, nocturnal activity, or that occur at low densities (Witmer, 2005). This is because species with these traits often have less than 60 observations, the minimum adequate number of observations for robust density estimation (Buckland, Cattanach, & Anganuzzi, 1992). In such cases, index methods such as camera trapping and spoor tracking may be better suited as they are able to obtain data across a wider range of species (Carbone et al., 2001; Keeping, 2014). However, indices have been criticised for being inappropriate proxies for true abundance (Anderson, 2001). This criticism is to a large extent aimed at addressing confounding factors which not only apply to index methods, but would affect any density estimation method (Bart, Burnham, Dunn, Francis, & Ralph, 2004). Thus, any monitoring program, including those

based on indices provided that they are rigorously designed (e.g. use probabilistic methods to select sampling sites), is in fact appropriate to assess trends in population size or density (Bart et al., 2004; Engemann, 2003).

Spoor tracking is an index widely used globally (Norris, Peres, Michalski, & Hinchliffe, 2008; Southgate & Moseby, 2008; Winterbach, Ferreira, Funston, & Somers, 2016). However, to date, this method has mostly been used for monitoring carnivore mammals (Bauer, Schiess-Meier, Mills, & Gusset, 2014; Fabiano, 2007; Gusset & Burgener, 2005) owing to the difficulty detecting and counting them by other means. Substantial effort has been made towards gaining a better understanding of the relationship between large carnivore spoor indices and true density. Strong correlations have been noticed between spoor indices and independent density estimates of large carnivores (from direct monitoring of individuals and intensive collaring studies) using linear calibration equations (Funston et al., 2010; Stander, 1998; Winterbach et al., 2016). Based on the success of linear calibration models for large carnivores, Funston et al. (2001) tentatively suggested extending such calibrations to large herbivores. Ideally, such an approach would require separate species-specific linear calibration equations because differences in individual species movement ecology theoretically affect the slope of any linear model. However, the effort would be quite onerous, requiring multiple independent estimates of density for each species (Funston et al., 2001).

The Formozov-Malyshev-Pereleshin (FMP) formula provides a theoretical foundation for converting spoor indices to true density through the variable day range (Stephens, Zaumyslova, Miquelle, Myslenkov, & Hayward, 2006). It therefore makes possible the estimation of density without the necessity of making several independent estimates of density. The FMP has been used for decades in Russia to monitor a wider range of taxa including ungulates (Stephens et al., 2006), yet remains underappreciated outside the region. In Africa, it has so far only been applied in Botswana, generating density estimates in close agreement with independent aerial and line transect estimates (Keeping, 2014; Keeping et al., 2018). The FMP assumes that spoor density is a function of both the true density and day range of a species and is theoretically robust to variations

in patterns of animal movement paths (Keeping & Pelletier, 2014). Application of the FMP is challenged by the unavailability of accurate empirical day range estimates. However, day range estimates can be made using allometric scaling rules between body mass and day range (Keeping, 2014).

Spoor tracking is an exceptionally efficient means for communities to collect data for monitoring wildlife populations in southern Africa (Keeping et al., 2018), and in many areas, it has become routine. If such data could be interpreted as density and trends in abundance, it could be made more useful. We thus applied the FMP formula using both empirical and allometric day range estimates to spoor data collected largely by community members of the Salambala Conservancy, in north-east Namibia, for the period between 2010 and 2016, to determine and assess trends in density for a range of mammal species.

2 | METHODS

2.1 | Study area

The Salambala Conservancy is located in north-eastern Namibia opposite the Chobe National Park in Botswana (Figure 1). The conservancy encompasses an area of 930 km². The climate is characterised by a tropical climate with high temperatures and heavy rainfall during the rainy season between December and March. Average monthly temperatures are of 30°C and annual rainfall of 620 mm (Laamanen & Otsu, 2002). The conservancy's source of water is the Chobe River, which runs along the border of the conservancy and separates it from the Chobe National Park. Animals are able to migrate freely between the two areas by crossing the river.

The area is characterised by floodplains and dry sandy areas. Floodplains have a lush grass cover and sandy areas open woodlands dominated by *Colophospermum mopane* (Mopane) along with *Baikiaea plurijunga* (Teak), *Guibourtia coleosperma* (False Mopane), *Terminalia sericea* (Silver Terminalia), *Burkea africana* (Wild Sringa), *Combretum* spp., and *Acacia* spp. The soil is mostly deep sand with a few floodplain areas of loamy clay to pure clay (Laamanen & Otsu, 2002).

Herbivore species inhabiting the conservancy include *Syncerus caffer* (African buffalo), *Loxodonta africana* (African elephant), *Connochaetes taurinus* (blue wildebeest), *Sylvicapra grimmia* (common duiker), *Aepyceros melampus* (common impala), *Taurotragus oryx* (eland), *Giraffa camelopardalis* (giraffe), *Tragelaphus strepsiceros* (greater kudu), *Equus quagga* (plains zebra), *Phacochoerus africanus* (warthog) and *Kobus ellipsiprymnus* (waterbuck). Carnivore species include *Crocuta crocuta* (spotted hyena), *Panthera leo* (African lion) and *P. pardus* (leopard).

2.2 | Data collection

Spoor surveys were conducted annually over 2 days during the dry season (September). Surveys were conducted along 13 parallel transects running north to south, and three perpendicular transects crossing eight of the 13 transects (Figure 1). Transect lengths ranged from 7 to 18 km (13.5 ± SD 4.2 km), totalling 215 km per annum. Transects did not follow any trails, so we assumed that animal interceptions with transects were random. Transects traversed all habitat types in the conservancy, traversing mostly sandy soils with smaller patches of clay substrate. While this could introduce variations in spoor detection, the ability of indigenous trackers has proven to be highly accurate under different environmental conditions (Stander, Ghau, Tsisaba, & Oma, 1997).

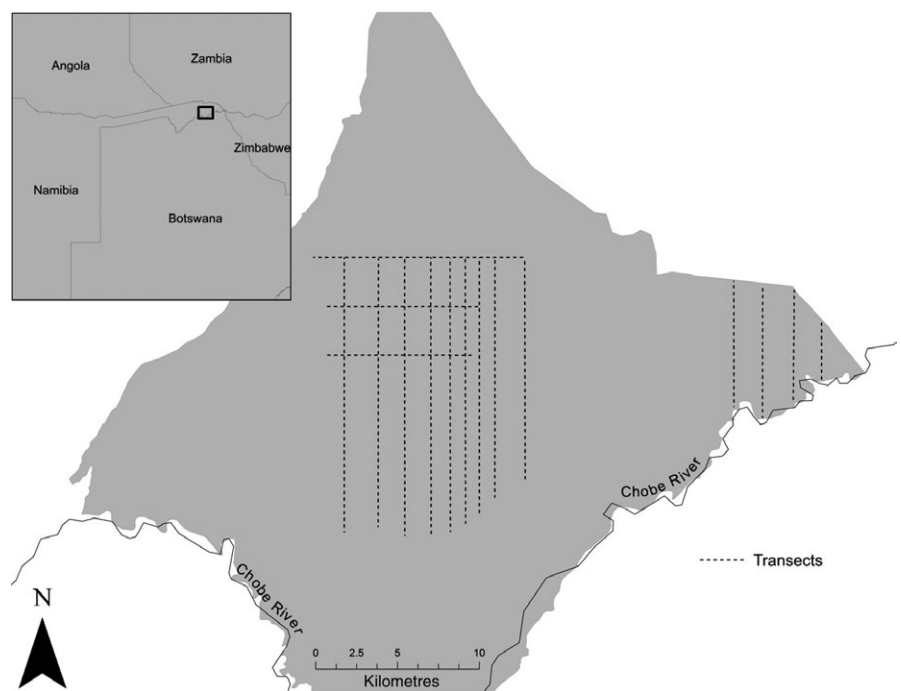


FIGURE 1 Map of the study area in relation to Namibia and Southern Africa and sampling transects ($n = 16$)

Transects were traversed by a team of 3 or 4 surveyors on foot commencing at 6:30 a.m. and ending upon completion of the transect (ranging from 8 a.m. to 11:00 a.m.). Surveyors included a combination of Ministry of Environment and Tourism (MET) rangers, local community game guards and trained local community members. The community game guards were all expert trackers. The spoor survey was conducted by the same observers simultaneously with line transect sampling. Upon detecting a spoor, the following was recorded: geographic location, species and the number of spoor detected. All ungulate and large carnivore species were recorded. Surveyors recorded spoors that expert trackers determined to have been made by different individuals within the last 24 hr, and disregarded duplicate spoors. Spoor assumed to have been made by an individual animal that was directly observed were also disregarded, as these direct sightings were recorded for distance sampling estimation. Accurate FMP estimates require all spoor intersections with transects to be recorded, including multiple re-crossings by the same individual animals (Keeping & Pelletier, 2014). We acknowledge the potential undercounting bias introduced by our data collection procedures. This undercounting bias may have been counteracted by the proximity of parallel transects, and perpendicular intersecting transects, whereby individual animals were presumably recorded on separate transects.

2.3 | Density calculations

Species-specific annual density estimates were determined as $D = (\pi/2)(x/S\hat{M})$, where D = density (km^2), x = number of spoor intersections on a transect, S = length of the transect and \hat{M} = average day range estimate of a species (km). Bootstrapping was applied to the x/S (spoor intersects per length of transect) values using R v.3.2.1 (R Core Team, 2017). Each bootstrap randomly sampled the x/S value from one of the 16 transects, with replacement, where the sample size of each

bootstrap was equal to the number of transects. Resampling probability of transects was calculated by dividing transect length by total area surveyed for the respective year. The mean of each bootstrap iteration was then determined until 5,000 mean values of x/S were created. These were randomly combined with bootstrapped mean day range estimates (\hat{M}) into the FMP formula to give 5,000 density estimates. Percentile confidence intervals (CI) were determined using the function *boot.ci* from the package *boot* version 1.3-19 in R v.3.4.1 (R Core Team, 2017).

Values for \hat{M} were either derived using allometric relationships (after Carbone, Cowlshaw, Isaac, & Rowcliffe, 2005) or empirical estimates obtained from published and unpublished sources (Table 1). \hat{M} estimates obtained from the literature were either from populations living nearby the study sampling area (i.e. Chobe National Park) or living in similar conditions. This was to minimise error as \hat{M} tends to vary with resource availability and thus differs among populations occurring in different habitats (Leggett, 2009; McQualter, Chase, Fennessy, McLeod, & Leggett, 2015). Only \hat{M} estimates obtained during the dry season were used to coincide with this study sampling period. Empirical \hat{M} estimates were determined by applying the Euclidean distance formula to GPS data available for 21 African buffalo (Naidoo, Preez, Stuart-Hill, Jago, & Wegmann, 2012) and five Plains zebra (Bartlam-Brooks, Beck, Bohrer, & Harris, 2013). Buffalo collars were programmed to take four GPS fixes per day (941 tracking days, 3,764 fixes) while zebra collars recorded one fix per hour (190 tracking days, 4,560 fixes). These day ranges were then bootstrapped 5,000 times with replacement, and the resulting mean day ranges were randomly combined with bootstrapped mean x/S values in the FMP formula.

Nine \hat{M} values were estimated allometrically. A least-squares linear regression model was fitted on the \log_e day range (km) and \log_e body mass (kg) of 22 species belonging to the order Artiodactyla (Carbone et al., 2005). These 22 pairs of body mass and day ranges were then

Species	\hat{M} (km \pm SD)	Source	Body Mass (kg)
African buffalo	6.54 \pm 3.73	Naidoo et al. (2012)	625
	4.75 \pm 1.57	Allometrically derived	
African elephant	9.12 \pm 5.11	Leggett (2009)	4,400
Blue wildebeest	4.79 \pm 0.70	Allometrically derived	215
Common duiker	2.5 \pm 1.03	Allometrically derived	16
Common impala	3.64 \pm 0.61	Allometrically derived	45
Eland	5.8 \pm 1.23	Allometrically derived	575
Giraffe	6.2 \pm 4.91	McQualter et al. (2015)	1,005
	6.45 \pm 1.69	Allometrically derived	
Greater kudu	4.85 \pm 0.72	Allometrically derived	215
Plains zebra	10.67 \pm 6.10	Bartlam-Brooks et al. (2013)	315
Spotted hyena	26.5 \pm 1.7	Mills (1990)	68
Warthog	3.93 \pm 0.56	Allometrically derived	70

TABLE 1 Surveyed mammal species, mean daily range movement \hat{M} (km) \pm standard deviation (SD) estimates, literature sources (for empirical day ranges) and body masses taken from Stuart and Stuart (2001)

resampled 5,000 times, with each iteration using sample sizes of $n = 22$ and sampling with replacement. At each iteration, a linear regression was fitted to the resulting sample, of which the slope and intercept were recorded, resulting in 5,000 pairs of intercept and slope values. Species which lacked day range estimates from the literature had their \log_e body mass plotted against bootstrapped slope and intercept pairs, resulting in 5,000 estimates of \hat{M} , which were combined with the 5,000 x/S values to give a range of density estimates from which the mean and CI for density were taken. Body mass values were taken from Stuart and Stuart (2001) using the average value between male and female.

Distance sampling density estimates were also calculated for each year by the Namibian Association of CBNRM Support Organizations (NACSO). Distance estimates use sighting data from the three most recent count years to achieve sufficient sightings per species ($n = 60$) (e.g. 2016 estimates are comprised of 2014, 2015 and 2016 surveys). The data are available online at <http://www.nacso.org.na/resources/game-count-data>. To compare precision between FMP and distance estimates, CI length was calculated as percentage of the mean for each method with lower values indicating higher precision (Barnes, 2002).

2.4 | Trend analysis

To determine trends in density from 2010 to 2016, we used a generalised additive model (GAM; Wood, 2006) to smooth the data, thus lessening the influence of annual fluctuations and allowing for a more reliable indicator of trends (Di Fonzo, Collen, & Mace, 2013). GAM is more suitable when dealing with relationships that are nonlinear and nonmonotonic, which can often be the case for ecological time series data (Fewster, Buckland, Siriwardena, Baillie, & Wilson, 2000). Furthermore, GAM does not restrict the functional form of the relationship between variables and can integrate a wider range of probability distributions (Guisan, Edwards, & Hastie, 2002).

General additive models assumed a nonhomogeneous Gaussian distribution, with density estimates being a function of survey years and mean annual rainfall values. The model's smoothness parameter was set to 2 based on the recommended value of 0.3 times the length of the time series ($n = 7$) (Fewster et al., 2000). GAM analyses were conducted using the package *mgcv* version 1.8–20 in R v.3.4.1 (R Core Team, 2017). Average rainfall values for each year from 2010–2016 were used (630, 510, 650, 470, 590, 340, 500 mm per year, respectively).

To determine whether a trend in density was statistically significant, we used an informal test described by Buckland et al. (1992). They indicate that if the 85% CI associated with two years in a series do not overlap, the magnitude of difference between the abundance estimates is considered to be significant at roughly the 5% level. A CI of exactly 83.4% achieves a 5% significance level if abundance estimates have equal coefficients of variation (CV); however, if one estimate has a CV twice the magnitude of the other, then an 85.6% CI corresponds to a 5% significance level (Buckland et al., 1992). Thus, using an 85% CI

we allow for differences in CV. Selected years are assumed to be independent and normally distributed with comparatively sized standard errors. We chose the first and last years in the time series.

2.5 | Simulations

Simulations were conducted to assess the effect on trends in density resultant from surveyors failing to record any spoor believed to have been created by a directly sighted individual. An unknown number of direct sighting data represented unrecorded spoor data. Thus, we created an additional data set in which all direct sightings were considered as spoor data (100%) and re-calculated density estimates. GAM models were then applied to the resulting density estimates, and retrieved trends were compared to our original trends. Here, we included only species which had ≥ 10 direct sightings.

All analyses were conducted in R v.3.4.1 (R Core Team, 2017).

3 | RESULTS

3.1 | Density calculations

Across the seven years, 17 total mammal species were recorded ($13 \pm SD 1$ per annum). Of these, annual density estimates were derived for only 10 species, as the other seven (buffalo, jackal, steenbok, leopard, reedbuck, roan and waterbuck) either had very low spoor detections (3 ± 1) or were only detected in very few years (range 2–4). Species with the highest average annual densities (100 per km^2) were common impala ($34.5 \pm SE 4.0$), blue wildebeest ($23.8 \pm SE 4.7$), common duiker ($16.1 \pm SE 1.3$) and greater kudu ($15.2 \pm SE 1.4$) (Table 2). Species with the lowest densities were eland ($5.4 \pm SE 0.6$), giraffe ($3.9 \pm SE 0.3$) and Spotted hyena ($0.2 \pm SE 0.03$) (Table 2).

3.2 | Trend analysis

General additive models explained $\geq 75\%$ of the variation for blue wildebeest, eland, duiker, giraffe, impala and warthog population time series, between 40% and 75% for elephant and zebra, and $< 30\%$ for kudu and Spotted hyena (Table 3). GAM models showed a negative temporal trend for three species (eland, elephant and warthog), and stable or positive temporal trends for the other seven species (blue wildebeest, common impala, duiker, giraffe, hyena, kudu and zebra) (Figure 2). Trends for blue wildebeest, impala and giraffe showed a recent increase after having declined in earlier years. None of these trends were significant as the 85% CI between 2010 and 2016 overlapped for all species.

3.3 | Simulations

General additive models based on simulated data sets showed increases for blue wildebeest, impala and giraffe, and decreases for

TABLE 2 Annual density estimates with 95% confidence intervals (CI) determined using Formozov–Malyshev–Perelshin for 10 wildlife species in the Salambala Conservancy in northern Namibia. N/A corresponds to years where no spoor were detected for a given species

Species	Density per 100 km ² (95% Confidence Intervals)									
	2010	2011	2012	2013	2014	2015	2016			
African elephant	18.2 (1.8–65.6)	32.4 (5.0–111.3)	21.1 (0.9–76.9)	34.0 (4.3–125.6)	4.5 (0.0–14.8)	8.7 (0.7–30.9)	9.5 (0.2–38.5)			
Blue wildebeest	21.6 (6.8–41.4)	35.7 (12.6–66.1)	7.6 (3.0–13.5)	24.4 (10.3–42.9)	24.7 (10.8–43.2)	12.9 (5.8–22.2)	43.1 (16.5–80.1)			
Common duiker	14.4 (5.6–27.6)	15.9 (6.1–31.1)	13.9 (4.8–28.4)	11.6 (4.1–23.5)	15.6 (3.2–42.5)	19.7 (6.9–39.6)	22.1 (8.11–44.5)			
Common impala	32.3 (17.9–50.8)	38.2 (20.1–62.0)	25.2 (8.7–53.1)	26.3 (12.3–44.2)	23.5 (9.2–46.5)	45.5 (22.9–74.5)	50.4 (28.6–79.0)			
Eland	N/A	N/A	7.3 (2.3–14.7)	6.3 (2.7–11.4)	4.2 (1.0–8.9)	5.5 (2.1–10.6)	4.1 (1.4–8.1)			
Giraffe	12.3 (1.1–47.8)	12.6 (1.5–53.3)	9.9 (1.0–42.1)	8.9 (0.7–35.0)	8.5 (0.7–38.6)	7.5 (0.7–32.8)	12.5 (0.8–51.5)			
Greater kudu	19.2 (10.2–31.5)	21.0 (11.8–33.6)	16.7 (8.9–26.5)	13.7 (7.4–22.4)	15.4 (8.3–25.6)	15.7 (9.8–23.4)	20.6 (13.0–30.6)			
Plains zebra	5.0 (0.0–27.2)	10.1 (0.0–48.1)	12.7 (0.0–63.2)	5.1 (0.0–21.5)	26.9 (0.0–125.2)	4.7 (0.0–21.1)	4.5 (0.0–24.4)			
Spotted hyena	0.08 (0.02–0.2)	0.28 (0.1–0.5)	0.16 (0.02–0.3)	0.05 (0.0–0.1)	0.15 (0.02–0.3)	0.28 (0.1–0.4)	0.14 (0.00–0.3)			
Warthog	9.6 (4.6–16.0)	11.4 (6.6–17.4)	5.6 (2.5–9.9)	5.6 (1.3–12.0)	5.8 (1.5–12.2)	8.5 (4.4–14.0)	4.7 (1.9–8.3)			

elephant, warthog and zebra. Kudu trends showed a decrease in early years (2010–2013), followed by a recovery in the second half of the time series (2013–2016) (Figure 3). The models explained a substantial amount of variation in the data (92%–75%) for blue wildebeest, giraffe, warthog and impala and explained less than 50% of the variation for kudu, zebra and elephant (Table 4). None of these trends were significant as all 85% CI overlapped between 2010 and 2016 for all species.

3.4 | Comparison between spoor and distance survey estimates

Density estimates between spoor and distance surveys showed relative agreement for most species (Figure 4). CIs showed large overlap between the two methods, with the largest discrepancies seen in impala, zebra and warthog density estimates. Comparison of precisions showed the methods to produce similar results, with a mean difference in precision of 77%. Of the 29 comparisons, distance sampling estimates were more precise in 15 cases, while FMP estimates were more precise in 13 cases, and one case resulting in equal precision (Table 5).

4 | DISCUSSION

An integral component underpinning sustainable utilisation of natural resources is monitoring. In this study, the FMP approach was applied for the first time to ecological data collected largely by community members in a communal conservancy in Namibia to estimate and explore trends in density. Through achieving density estimates for 10 species, including cryptic species, we demonstrated the value of the FMP's application to spoor count data for monitoring a wide range of species in different functional groups. Findings suggest a general but nonsignificant positive temporal trend for five species (blue wildebeest, common impala, common duiker, giraffe and kudu) and a negative trend for four species (eland, elephant, plains zebra and warthog). Nonetheless, the derived density estimates and observed temporal trends suffer from several limitations in both the spoor index and day range components of density estimation using the FMP formula.

Firstly, density estimates were likely underestimated because the sampling protocol used at Salambala and other conservancies in Namibia requires trackers to record individual animals' spoor once only, and to disregard spoor linked to animals directly sighted. Thus, many spoor-transect interceptions that are required for accurate FMP density estimation are unrecorded by present sampling protocols. This is illustrated by the zebra data set, whereby a potential total of 10,174 spoor were not recorded over the seven years (10,828 direct sightings – 654 spoor). The impact of this shortcoming on density estimates is therefore potentially substantial in confounding trends if detectability varied between years.

Species	Variation explained (%)	85% CI (2010)	85% CI (2016)
African Elephant	65	2.7–27.3	0.5–18.4
Blue Wildebeest	99	10.0–35.5	22.0–69.0
Common duiker	84	7.2–23.6	10.3–36.6
Common impala	90	21.2–44.8	32.8–70.3
Eland	68	3.1–12.2 ^a	1.9–6.7
Giraffe	89	1.5–17.0	1.3–17.6
Greater Kudu	63	12.2–27.7	14.6–27.3
Plains Zebra	45	0.0–16.1	0.0–17.2
Spotted hyena	25	0.03–0.1	0.03–0.3
Warthog	75	5.7–13.9	2.6–7.2

^aEland time series begins in 2012 rather than 2010.

Secondly, both accuracy and precision of density estimates were likely affected by applying allometrically derived substitutes for empirical day range estimates. We were constrained to this approach by the general scarcity of precise, regional, day range estimates, particularly for herbivores species. The sources used likely failed to capture all heterogeneity in movements. While the use of allometric relationships to derive day range estimates is a scientifically valid method (Aguilar-Trigueros, Rillig, & Crowther, 2017; Carbone et al., 2005; Keeping, 2014), our allometric movement estimates captured less variation compared to movement estimates based on empirical methods such as tracking or GPS collars. This is because a single mean estimate of day range for each species was used; thus, the allometric approach utilised inter-species variation rather than within-species variation. For example, empirical GPS tracking data for African buffalo had higher variation in day range (SD 3.73 km) than those derived allometrically in this study (SD 1.57 km). Thus, allometrically derived movement estimates led to an overestimate in density estimate precision. Future efforts to utilise allometric estimates of day range applied to FMP could be improved by creative analyses that incorporate the within-species variation in day range to estimate variance more fairly.

Thirdly, empirical movement estimates for mammal species are typically determined from telemetry data with coarse temporal resolutions (Owen-Smith, Fryxell, & Merrill, 2010; Naidoo et al., 2012). This is also a potential source of bias. In this study, time intervals between GPS fixes were ≥ 1 hr (Bartlam-Brooks et al., 2013; Naidoo et al., 2012). GPS fixes set to such intervals can severely underestimate total day range (Rowcliffe, Carbone, Kays, Kranstauber, & Jansen, 2012), as they fail to capture fine-scale movement, such as movement during foraging (Owen-Smith et al. 2010). These same constraints apply to literature-based range estimates as these are often based on telemetry data. Underestimating day range results in an overestimation of FMP-based density. Possibilities to correct this include technological advances in micro-transmitters that record animal movements at sub-second intervals (Wilson, Shepard, & Liebsch, 2008).

However, in many tracking environments in which the FMP can be applied, it also possible to simply follow (trail) the tracks of animals using hand-held GPS units to obtain near-perfect tracings of their day ranges (Keeping & Pelletier, 2014; Stephens et al., 2006).

The main limitation and potentially confounding factor to estimating trends was our assumption that day ranges remained constant from 2010 to 2016. Any trends were thus resulting entirely from the spoor count component of FMP density estimates while inter-annual species day ranges were assumed constant. The degree to which this assumption is likely to have been violated implicates our confidence in trends. There were fluctuations in annual rainfall (CV 20%) across the study period. Such variable rainfall influences ungulate movement in response to resource availability (Ogutu, Piepho, Dublin, Bhola, & Ried, 2008; Ogutu et al., 2016). Notably, the assumption of constant day range is implicitly assumed whenever spatial-temporal comparisons of repeat spoor surveys are made, including index-density calibration approaches (e.g. Winterbach et al., 2016), unless re-calibrated to local conditions every survey. The extent by which average day range fluctuates from year to year requires further investigation.

Trends generated from the simulated data set (all spoors and all direct sightings) retrieved similar trends as those based only on spoors. This suggests sampling error was minimised as observers were relatively consistent year to year omitting tracks made by animals that were also directly sighted. Indeed, many of the same community members participated in multiple surveys across the seven years and a consistent protocol was used. For these reasons, we are confident that observed trends most likely do reflect true trends for these species.

Comparisons between FMP and distance sampling showed that most estimates and CIs between the two methods were in relative agreement. Precision of estimates showed little difference, with distance sampling producing more precise estimates in 15 of the 29 cases, but representing data from three years. However, a linear relationship between CIs and density estimates has been shown by Barnes (2002), whereby CIs tend to decrease as estimates increase.

TABLE 3 Summary of species-specific generalised additive model analysis that includes variation explained and 85% confidence interval (CI) for years 2010 and 2016. Variation explained values represent the degree of the model fit to the data. Lack of overlap between confidence intervals of first and last time series points suggests a significant ($p \leq 0.05$) trend

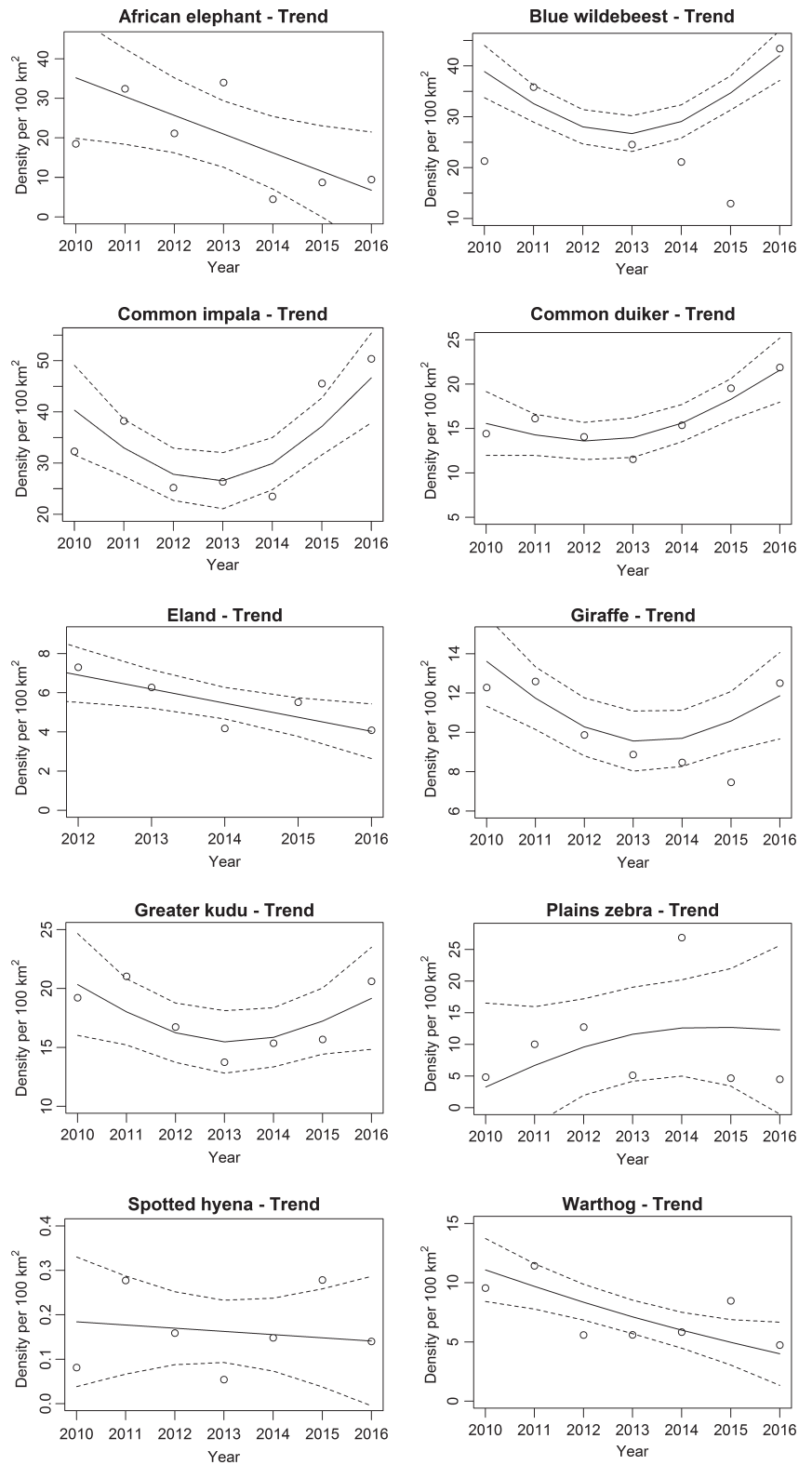


FIGURE 2 Species-specific trend in annual density estimates based on generalised additive (GAM) models. Dotted lines represent the GAM model 95% confidence intervals for the entire time series. For eland, the distance between the confidence intervals and the GAM model line is too small to distinguish between the two

As FMP density estimates were lower than distance sampling estimates in 25 of the 29 comparisons, higher precision from FMP results should be expected if all spoors had been recorded during sampling. Zebra and impala density estimates varied considerably between the two methods, with FMP producing lower estimates. Both species exhibit gregarious behaviour, therefore making for

improved probability of direct sighting, and thus a decrease in spoor data due to the sampling protocol excluding tracks of animals directly sighted.

Distance sampling density estimates have been calculated using a 3-year moving average of the sampling data due to insufficient sightings in annual surveys. Using composite estimates creates difficulties regarding

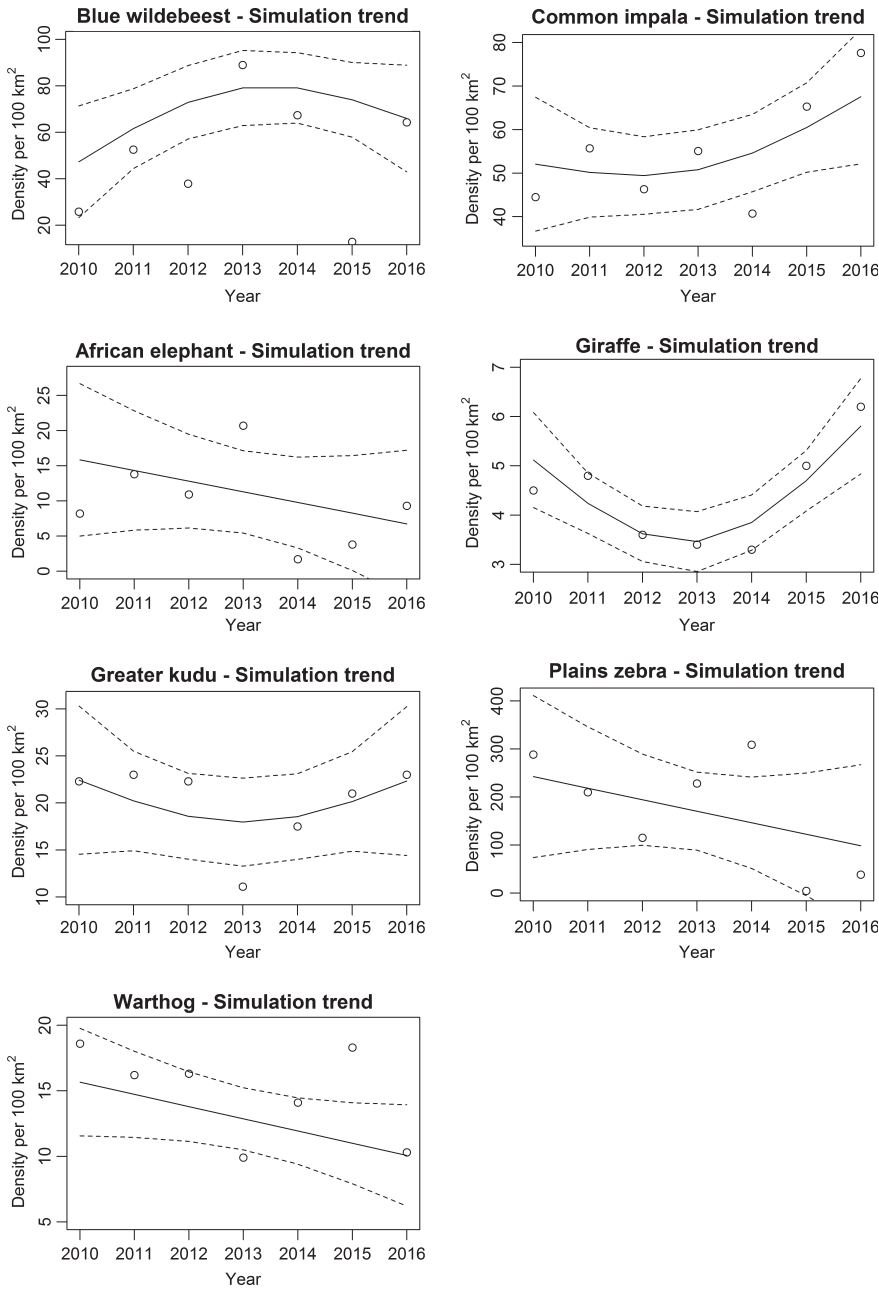


FIGURE 3 Species-specific trend in annual density estimates based on generalised additive (GAM) models. Models use complete data from both spoor and observational data sets (simulation 100%). Dotted lines represent the GAM model 95% confidence intervals for the entire time series. For eland, the distance between the confidence intervals and the GAM model line is too small to distinguish between the two

Species	Variation Explained (%)	85% CI (2010)	85% CI (2016)
Blue Wildebeest	92	11.5–42.3	35.6–96.8
Common impala	75	30.1–60.0	54.2–123.3
Elephant	39	3.6–52.4	2.9–64.5
Giraffe	88	2.5–8.2	2.4–11.0
Greater Kudu	42	14.5–31.5	16.3–33.9
Plains Zebra	46	0.0–930.3	0.0–124.3
Warthog	78	12.3–26.0	5.0–18.2

TABLE 4 Summary of species-specific generalised additive model analysis for simulated data sets that includes variation explained and 85% confidence interval (CI) for years 2010 and 2016. Variation explained values represent the degree of the model fit to the data. Lack of overlap between confidence intervals of first and last time series points suggests a significant ($p \leq 0.05$) trend

the interpretation of results, as well as possibly compromising their validity. Moving averages mask sudden changes in the data within certain years, thus leading to potential bias in decisions made on an annual basis

(e.g. hunting quotas). Pooling data from three survey years also implies that distance sampling requires three times the current sampling effort in order to calculate robust annual density estimates.

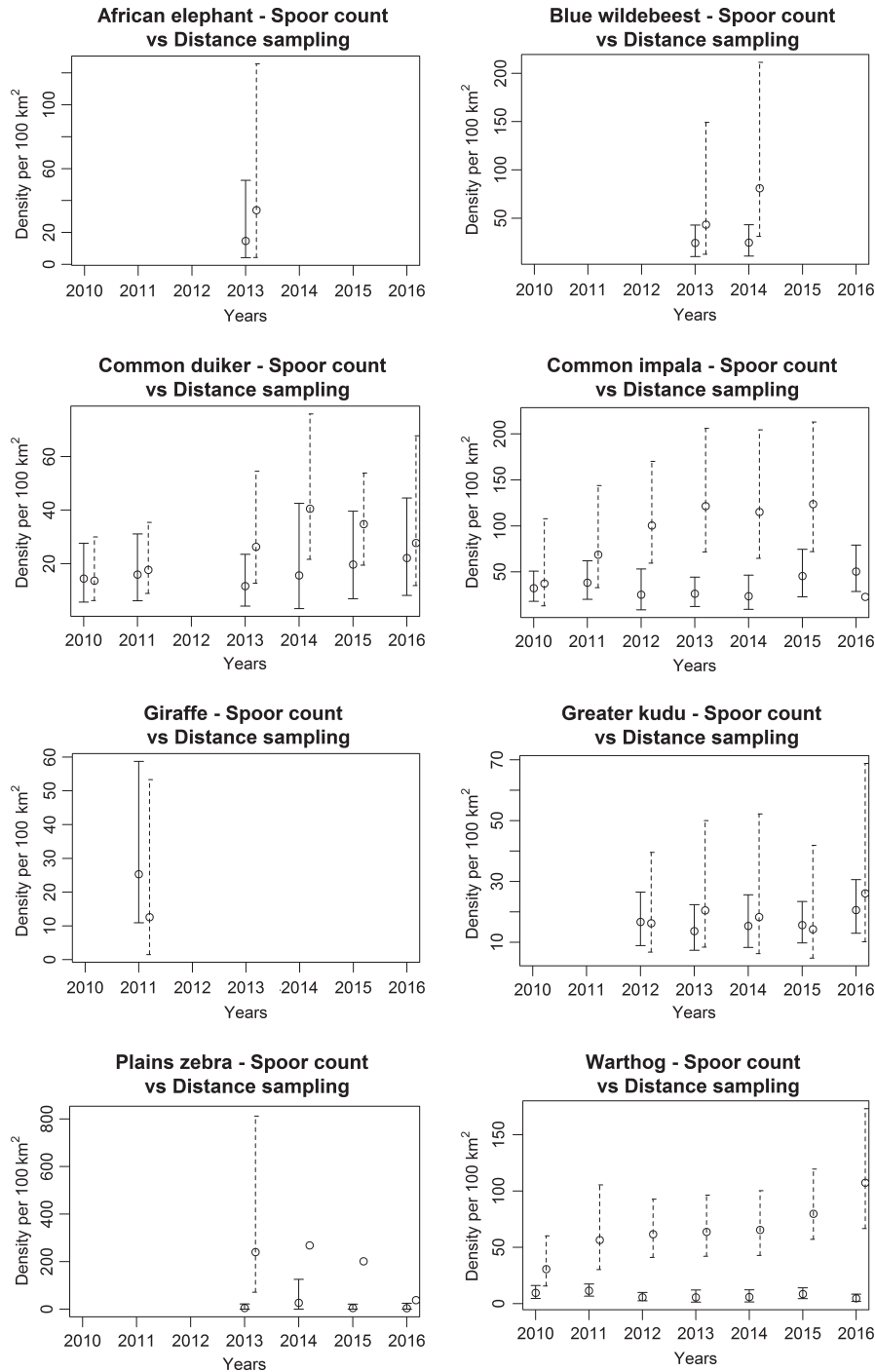


FIGURE 4 Species-specific annual density estimates and 95% confidence intervals comparing spoor counts (solid line) to distance sampling (dotted line). Years with no estimates are years where distance sampling was unable to produce estimates due to insufficient sightings. Estimates without confidence intervals are due to intervals not being reported

By using the FMP, we were able to derive estimates for species that are elusive (e.g. carnivores) or occurring in low densities. In only two cases could densities not be calculated using spoor data (eland in 2010 and 2011), while distance sampling data combined from three years failed to calculate densities in many cases. The FMP's ability to monitor multiple species is worth noting as this is a prerequisite for monitoring community structure (Cromsigt &

Oloff, 2008), functional diversity and, consequently, in preserving ecosystem functions (Cadotte, Carscadden, & Mirotnick, 2011).

Temporal trends suggest that six of the 10 species populations are stable. This is of importance to conservancies and various stakeholders as on one hand it reflects the effects of current management efforts, and on the other the need to concentrate efforts to species identified as potentially declining. Species

Species	Percentage confidence length						
	2010	2011	2012	2013	2014	2015	2016
African elephant							
Spoor count	351	328	360	357	329	347	403
Distance sample	N/A	N/A	N/A	330	N/A	N/A	N/A
Blue wildebeest							
Spoor count	160	150	138	134	131	127	148
Distance sample	N/A	N/A	N/A	315	222	N/A	N/A
Common duiker							
Spoor count	153	157	170	167	252	166	165
Distance sample	175	150	N/A	159	134	99	202
Common impala							
Spoor count	102	110	176	121	159	113	100
Distance sample	253	161	110	111	121	113	N/A
Giraffe							
Spoor count	380	411	415	385	446	428	406
Distance sample	N/A	189	N/A	N/A	N/A	N/A	N/A
Greater Kudu							
Spoor count	111	104	105	109	112	87	85
Distance sample	N/A	N/A	201	203	251	259	225
Plains zebra							
Spoor count	544	476	498	422	465	449	542
Distance sample	N/A	N/A	N/A	309	N/A	N/A	N/A
Warthog							
Spoor count	119	95	132	191	184	113	136
Distance sample	146	133	83	85	88	78	99

TABLE 5 Percentage confidence length for spoor count and distance sampling density estimates. Calculated as confidence interval length divided by mean density estimate × 100. Lower values indicate higher levels of precision

which showed steep but nonstatistically significant decreases in population size were eland, elephant, warthog and zebra. Eland was re-introduced into the conservancy in 2012 and the population may have not yet established itself. It is also possible that the population is failing to persist in the study area or that other factors may be suppressing its growth. Human encroachment, poaching and policy do negatively affect ungulate abundance (Ogutu et al., 2016). Eland in particular are sensitive to human disturbance, highly sought after for their meat, and hunted readily without firearms (D. Keeping *personal observation*). Warthog decreases may be due to retaliation and or poaching, as warthogs can cause agricultural damages and are often hunted opportunistically (Kalher & Gore, 2015; Swanepoel, Leslie, & Hoffman, 2016). Elephant populations have declined across the African continent (with the exception of a few national park areas) (Chase et al., 2016) with poaching possibly being a major driver in Namibia (Nakale, 2017). Zebra declines have been linked to fluctuations in rainfall (Georgiadis, Hack, & Turpin, 2003), and as the largest decrease in population occurred in the year with the least rainfall, it is possible that the observed trend is linked with rainfall patterns. Since Salambala Conservancy is not fenced in any way, it is possible that the zebra population relocated into

the Chobe National Park during the recent drier years. Hyaena are often implicated in human-wildlife conflict incidents and removed at times (NACSO, 2016). For the 10 stable species, the lack of relationship between dry season density estimates and annual rainfall may be because these species respond differently to rainfall patterns (Ogutu et al., 2008). Thus, these findings demonstrate that there is a need to acquire improved density estimates and implement a more fine-scale demographic monitoring that can allow for proper assessment of how these species respond to environmental changes. The FMP approach, given an adjustment of spoor survey protocol and improved day range estimation, could make a valuable contribution to future monitoring and the inference derived therefrom.

Only two species, zebra and blue wildebeest, showed trends that differed between those retrieved using only the spoors data set versus the simulated data set. We suggest the simulated trend is likely more accurate for both species given the large proportion of spoor neglected for direct sightings. Also, the gregarious behaviour of these two species may lead them to be undercounted by their spoor if group sizes are large (Keeping et al., 2018), and since they are both highly visible and relatively abundant, direct sightings methods might rather be preferred (Caro, 2016).

In conclusion, by applying the FMP formula to routine monitoring data collected by community members of a communal conservancy it was possible to derive density estimates for 10 species recorded in the study area between 2010 and 2016. This was an improvement over the currently employed distance method which only generated density estimates for eight species, of which only two species had density estimates for the entire range of 2010–2016. These findings demonstrate the potential of this technique to monitor a wider number of species than the conservancy's distance surveys. However, as the reliability of FMP depends on appropriate day range estimates which remain a substantial knowledge gap, we recommend double sampling using simultaneous line transects. We also recommend that future surveys in this and other conservancies record all spoor regardless of individual identity or whether those animals are doubly recorded as line transect observations and that accurate day range estimates are obtained over a period of several years. The latter might be accomplished through local experienced trackers trailing animals. If these recommendations are met, then the FMP method could be an invaluable tool for monitoring and conserving multispecies.

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REFERENCES

- Aguilar-Trigueros, C. A., Rillig, M. C., & Crowther, T. W. (2017). Applying allometric theory to fungi. *The ISME Journal*, 11, 2175–2180. <https://doi.org/10.1038/ismej.2017.86>
- Anderson, D. R. (2001). The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin*, 29(4), 1294–1297.
- Barnes, R. F. W. (2002). The problem of precision and trend detection posed by small elephant populations in West Africa. *African Journal of Ecology*, 40, 179–185. <https://doi.org/10.1046/j.1365-2028.2002.00376.x>
- Bart, J., Burnham, K. P., Dunn, E. H., Francis, C. M., & Ralph, C. J. (2004). Goals and strategies for estimating trends in landbird abundance. *Journal of Wildlife Management*, 68, 611–626.
- Bartlam-Brooks, H. L. A., Beck, P. S. A., Bohrer, G., & Harris, S. (2013). In search of greener pastures – using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences*, 118, 1–11. <https://doi.org/10.1002/jgrg.20096>
- Bauer, D., Schiess-Meier, M., Mills, D. R., & Gusset, M. (2014). Using spoor and prey counts to determine temporal and spatial variation in lion (*Panthera leo*) density. *Canadian Journal of Zoology*, 92, 97–104.
- Buckland, S. T., Cattanach, K. L., & Anganuzzi, A. A. (1992). Estimating trends in abundance of dolphins associated with tuna in the eastern tropical Pacific Ocean, using sightings data collected on commercial tuna vessels. *Fishery Bulletin*, 90, 1–12.
- Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48(5), 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Carbone, C., Cowlshaw, G., Isaac, N. J. B., & Rowcliffe, M. (2005). How far do animals go? Determinants of day range in mammals. *The American Naturalist*, 165(2), 290–297. <https://doi.org/10.1086/426790>
- Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J. R., ... Wan Shahrudin, W. N. (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4, 75–79. <https://doi.org/10.1017/S1367943001001081>
- Caro, T. (2016). Guidelines for wildlife monitoring: savannah herbivores. *Tropical Conservation Science*, 9(1), 1–15.
- Chase, M. J., Schlossberg, S., Griffin, C. R., Bouche, P. J. C., Djene, S. W., Elkan, P. W., ... Sutcliffe, R. (2016). Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, 4, e2354.
- Cromsigt, J. P. G. M., & Olff, H. (2008). Dynamics of grazing lawn formation: An experimental test of the role of scale-dependent processes. *Oikos*, 117, 1444–1452. <https://doi.org/10.1111/j.0030-1299.2008.16651.x>
- Danielsen, F., Burgess, N. D., & Balmford, A. (2005). Monitoring matters: examining the potential of locally-based approaches. *Biodiversity and Conservation*, 14(11), 2507–2542.
- Di Fonzo, M., Collen, B., & Mace, G. M. (2013). A new method for identifying rapid decline dynamics in wild vertebrate populations. *Ecology and Evolution*, 3(7), 2378–2391. <https://doi.org/10.1002/ece3.596>
- Engemann, R. M. (2003). Mor on the need to get the basics right: Population indices. *Wildlife Bulletin*, 31, 286–287.
- Fabiano, E. C. (2007). Evaluation of spoor tracking to monitor cheetah abundance in central northern Namibia. Master's thesis. University of KwaZulu-Natal.
- Fewster, R. M., Buckland, S. T., Siriwardena, G. M., Baillie, S. R., & Wilson, J. D. (2000). Analysis of population trends for farmland birds using generalized additive models. *Ecology*, 81(7), 1970–1984. [https://doi.org/10.1890/0012-9658\(2000\)081\[1970:AOPFF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1970:AOPFF]2.0.CO;2)
- Funston, P. J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D. M., ... Ferreira, S. M. (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, 281, 56–65. <https://doi.org/10.1111/j.1469-7998.2009.00682.x>
- Funston, P. J., Herrmann, E., Babupi, P., Kruijer, A., Kruijer, H., Jagers, H., ... Kruijer, K. (2001). Kalahari Transfrontier Lion Project: Final Report. Submitted to South African National Parks and Botswana Department of Wildlife and National Parks.
- Georgiadis, N., Hack, M., & Turpin, K. (2003). The influence of rainfall on zebra population dynamics: Implications for management. *Journal of Applied Ecology*, 40(1), 125–136. <https://doi.org/10.1046/j.1365-2664.2003.00796.x>
- Guisan, A., Edwards, T. C., & Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: Setting the scene. *Ecological Modelling*, 157, 89–100. [https://doi.org/10.1016/S0304-3800\(02\)00204-1](https://doi.org/10.1016/S0304-3800(02)00204-1)
- Gusset, M., & Burgener, N. (2005). Estimating larger carnivore numbers from track counts and measurements. *African Journal of Ecology*, 43, 320–324. <https://doi.org/10.1111/j.1365-2028.2005.00581.x>
- Hausser, Y., Tagand, R., Vimercati, E., Mermod, S., & Fischer, C. (2016). Comparing survey methods to assess the conservation value of a community-managed protected area in western Tanzania. *African Journal of Ecology*, 55(1), 1–11.
- Kalher, J. S., & Gore, M. L. (2015). Local perceptions of risk associated with poaching of wildlife implicated in human-wildlife conflicts in Namibia. *Biological Conservation*, 189, 49–58. <https://doi.org/10.1016/j.biocon.2015.02.001>
- Keeping, D. (2014). Rapid assessment of wildlife abundance: Estimating animal density with track counts using body mass – day range scaling

- rules. *Animal Conservation*, 17, 486–497. <https://doi.org/10.1111/acv.12113>
- Keeping, D., & Pelletier, R. (2014). Animal density and track counts: Understanding the nature of observations based on animal movements. *PLoS ONE*, 9(5), e96598. <https://doi.org/10.1371/journal.pone.0096598>
- Keeping, D., Burger, J. H., Keitsile, A. O., Gielen, M., Mudungo, E., Wallgren, M., ... Foote, A. L. (2018). Can trackers count free-ranging wildlife as effectively and efficiently as conventional aerial survey and distance sampling? Implications for citizen science in the Kalahari, Botswana. *Biological Conservation*, 223, 156–169. <https://doi.org/10.1016/j.biocon.2018.04.027>
- Laamanen, R., & Otsu, M. (2002). Forest management plan for the Salambala conservancy core area. Retrieved from http://www.theeis.com/data/literature/Man_plan_Salambala.pdf
- Leggett, K. (2009). Daily and hourly movement of male desert-dwelling elephants. *African Journal of Ecology*, 48, 197–205. <https://doi.org/10.1111/j.1365-2028.2009.01101.x>
- McQualter, K. N., Chase, M. J., Fennessy, J. T., McLeod, S. R., & Leggett, K. (2015). Home ranges, seasonal ranges and daily movements of giraffe (*Giraffa camelopardalis giraffe*) in Northern Botswana. *African Journal of Ecology*, 54, 99–102.
- Mills, M. G. L. (1990). *Kalahari hyaenas: comparative behavioural ecology of two species*. London: Unwin Hyman.
- NACSO (2016). Game counts in Bwabwata & Zambezi. Retrieved from http://www.nacso.org.na/sites/default/files/Zambezi%20Game%20Count%20-%20East2016_0.pdf
- NACSO (2017). *Game counts in Bwabwata & Zambezi*. Retrieved from <http://www.nacso.org.na/sites/default/files/Zambezi%20Game%20Count%20-%20East%202017%20Final.pdf>
- Naidoo, R., Preez, D. P., Stuart-Hill, G., Jago, M., & Wegmann, M. (2012). Home on the range: Factors explaining partial migration of African buffalo in a tropical environment. *PLoS ONE*, 7(5), e36527. <https://doi.org/10.1371/journal.pone.0036527>
- Nakale, A. (2017). More than 240 elephants poached since 2014. *New Era Newspaper*. Retrieved from <https://www.newera.com.na/2017/07/24/more-than-240-elephants-poached-since-2014/>
- Norris, D., Peres, C. A., Michalski, F., & Hinchsliffe, K. (2008). Terrestrial mammal responses to edges in Amazonian forest patches: A study based on track stations. *Mammalia*, 72(1), 15–23. <https://doi.org/10.1515/MAMM.2008.002>
- Ogutu, J. O., & Owen-Smith, N. (2003). ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters*, 6(5), 412–419. <https://doi.org/10.1046/j.1461-0248.2003.00447.x>
- Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bholá, N., & Ried, R. S. (2008). Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *Journal of Animal Ecology*, 77(4), 814–829. <https://doi.org/10.1111/j.1365-2656.2008.01392.x>
- Ogutu, J. O., Piepho, H. P., Said, M. Y., Ojwang, G. O., Njino, L. W., Kifugo, S. C., & Wargute, P. W. (2016). Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: What are the causes? *PLoS One*, 11(9), e0163249.
- Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2267–2278.
- R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rowcliffe, M. J., Carbone, C., Kays, R., Kranstauber, B., & Jansen, P. A. (2012). Bias in estimating animal travel distance: the effect of sampling frequency. *Methods in Ecology and Evolution*, 3, 653–662.
- Southgate, R., & Moseby, K. (2008). Track-based monitoring for the deserts and rangelands of Australia. Threatened Species Network, WWF Australia. Retrieved from <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.462.6813&rep=rep1&type=pdf>.
- Stander, P. E. (1998). Spoor counts as indices of large carnivore populations: The relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology*, 35, 378–385. <https://doi.org/10.1046/j.1365-2664.1998.00313.x>
- Stander, P. E., Ghau, I. I., Tsisaba, D., & Oma, I. I. (1997). Tracking and the interpretation of spoor: A scientifically sound method in ecology. *Journal of Zoology*, 242(2), 329–341. <https://doi.org/10.1111/j.1469-7998.1997.tb05805.x>
- Stephens, P. A., Zaumyslova, O. Y., Miquelle, D. G., Myslenkov, A. I., & Hayward, G. D. (2006). Estimating population density from indirect sign: Track counts and the Formozov-Malyshev-Pereshin formula. *Animal Conservation*, 9, 339–348. <https://doi.org/10.1111/j.1469-1795.2006.00044.x>
- Stuart, C. T., & Stuart, M. D. (2001). *Field guide to mammals of Southern Africa* (3rd ed.). Cape Town: Struik Publishers.
- Swanepoel, M., Leslie, A. J., & Hoffman, L. C. (2016). Farmers' perceptions of the extra-limital common warthog in the Northern Cape and free state provinces, South Africa. *Wildlife Society Bulletin*, 40(1), 112–121. <https://doi.org/10.1002/wsb.617>
- Wilson, R. P., Shepard, E. L. C., & Liebsch, N. (2008). Prying into the intimate details of animal lives: Use of a daily diary on animals. *Endangered Species Research*, 4(1–2), 123–137. <https://doi.org/10.3354/esr00064>
- Winterbach, C. W., Ferreira, S. M., Funston, P. J., & Somers, M. J. (2016). Simplified large African carnivore density estimators from track indices. *PeerJ*, 4, e2662. <https://doi.org/10.7717/peerj.2662>
- Witmer, G. W. (2005). Wildlife population monitoring: Some practical considerations. *Wildlife Research*, 32, 259–263. <https://doi.org/10.1071/WR04003>
- Wood, S. N. (2006). *Generalized additive models: An introduction with R*. Boca Raton, FL: Chapman & Hall.

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