Research Article

Counting giraffes: A comparison of abundance estimators on the Ongava Game Reserve, Namibia

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Abstract

Camera-traps are a versatile and widely adopted tool for collecting biological data for wildlife conservation and management. While estimating population abundance from camera-trap data is the primarily goal of many projects, the question of which population estimator is suitable for analysing these data needs to be investigated. We took advantage of a 21 day camera-trap monitoring period of giraffes (*Giraffa camelopardalis angolensis*) on the Ongava Game Reserve (Namibia) to compare capture-recapture (CR), rarefaction curves and N-mixture estimators of population abundance. A marked variation in detection probability of giraffes was observed both in time and between individuals, with a skewed occurrence of animals at some waterholes. The mean daily visit frequency of waterholes by giraffes was $f = 0.25$ although they were less likely to be detected after they were seen at a waterhole. We estimated the population size to be 104 giraffes ($C_v = 0.02$) using the most robust reference estimator (CR). All other estimators deviated from the CR population size by $ca. -16$ to $> +106\%$. This was due the fact that these models did not account for the temporal and individual variations in detection probability. We found that modelling choice was much less forgiving for N-mixture models than CR estimators because the former leads to very variable and inconsistent estimations of abundance. Double counts were problematic for N-mixture models, challenging the use of raw counts (i.e. when individuals are not identified), to monitor the abundance of giraffes or of other species without idiosyncratic coat patterns.

Introduction

The on-going development and large-scale deployment of camera trapping technology offers a promising and appealing way for ecologists to collect a variety of biological data at an unprecedented scale and speed (Swanson et al., 2015). Habitat use, activity patterns and population abundance are now frequently studied using camera trap data (O'Connel et al., 2011; Trolliet et al., 2014). Sampling a population with camera-traps is indeed particularly useful and efficient (Wearn and Glover-Kapfer, 2019), even more so for species with idiosyncratic coat patterns from which individual identification is possible (e.g. Jackson et al., 2006; Karanth and Nichols, 1998; Stratford and Stratford, 2011). Camera trap data are increasingly used to estimate population abundance (Burton et al., 2015; Gilbert et al., 2021) but such data come with specific problems. Detection rate is not perfect, and sampling design and effort are likely different from physical captures (Hamel et al., 2013; Gilbert et al., 2021). While obtaining unbiased estimates of abundance is of central importance for conservation and wildlife management to set appropriate goals and policies (Anderson, 2001), the suitability of the currently available population abundance estimators for camera-trap data remains to be evaluated empirically.

For populations living in the wild, the main issue is of an underestimation of abundance because an unknown proportion of animals are missed during surveys, i.e. animal detection is not perfect (Strandgaard, 1967; Apollonio et al., 2010). Imperfect detection is the main reason why detection probability of individuals underpins most population abundance estimators (Seber, 1982; Schwarz and Seber, 1999). Past empirical studies showed how detection probability can vary in both time and space (Otis et al., 1978). For instance, detection probability

was reported to increase with habitat openness (Choquenot, 1995), vary between con-specifics with different behavioural repertoires (i.e. personalities, see Le Cœur et al., 2015, for an example on Siberian chipmunk *Tamias sibiricus*), decrease with the distance of animals from the observer (Burnham et al., 1980; Buckland et al., 2000), between observers themselves depending on their experience or motivation in spotting animals (Collier et al., 2007; Zett et al., 2022), and between camera trap brands or orientation (Rovero et al., 2013).

Accounting for these intrinsic and extrinsic sources of detection heterogeneity has profound consequences for the accuracy and precision of population abundance estimations (Veech et al., 2016). Currently, only a handful of population abundance estimators can account for the multiple sources of variability in detection probability, and most derive from either distance sampling (DS) and capture-recapture (CR). Both families of estimators can accommodate detection rate for known sources of variability like time of the year, habitat type, or sex and age of individuals (Pollock, 1980; Schwarz and Seber, 1999) while only the CR approach can model unmeasured or unknown sources of heterogeneity.

The reason why these two methods are not systematically implemented in the field is due to serious practical limitations. CR requires a substantial proportion of the population to be recognizable: for instance Strandgaard (1972) recommended that up to 2/3 of a roe deer (*Capreolus capreolus*) population should be marked to obtain robust results. In addition, the capture and marking of wild animals can raise ethical questions for endangered species. DS on the other hand, is quite sensitive to the sampling design (e.g. linear transects and coverage), and is sometimes difficult to carry out in dense tropical forests of Africa (Duckworth, 1998), or when human disturbance induces behavioural responses (see Elenga et al., 2020, on blue duikers *Philantomba monticola*). In other words, these two reference methods for estimating

animal abundance can rapidly become prohibitively expensive, time consuming and difficult to implement at large spatial scale for wildlife managers (Morellet et al., 2007).

By seeking to keep implementation costs low, practitioners often make use of easier-to-implement, cheaper methods to monitor wildlife populations at spatial scales compatible with wildlife management (Morellet et al., 2007). This choice often comes at the costs of using estimators with less flexibility in accounting for variability in detection rate. For instance, catch-per-unit effort (Leslie and Davis, 1939) or rarefaction curves (Petit and Valière, 2006) can return an estimate of population size from unmarked animals, but both assume constant detection rates for all individuals over the sampling period. A noticeable exception is the *N*-mixture model (Royle, 2004), which allows the separation of population size from detection probability using repeated counts of animals in time and space. The robustness and accuracy of *N*-mixture abundance estimators is, however, frequently questioned (Kéry, 2018).

For decades in large African national parks, a common practice has been to monitor wildlife using indices of population abundance of large herbivore species from direct (observation of animals) or indirect observations (observation of signs like tracks, faeces; Jachmann, 2002, 2012). Such indices can be obtained through road transects counts (with visibility issues), aerial counts (with visibility issues and high costs), and waterhole counts of various duration (with the risk of missing water-independent species). The underlying assumption of a constant detection rate has been advanced to be the main reason for indices of population abundance to fail at monitoring wildlife abundance reliably (Anderson, 2001). However, these indices might be suitable for use by managers following a validation test against a reference method (Morellet et al., 2007). While several studies show that not accounting for detection variability can indeed bias population abundance estimates (Dail and Madsen, 2011), the magnitude and direction of this bias is seldom quantified empirically.

The giraffe (*Giraffa camelopardalis ssp.*) is a charismatic species of conservation significance with decreasing populations in many parts of Africa (O'Connor et al., 2019). The assessment of local populations' conservation status and their long-term viability are however hampered by the many different ways abundance has been estimated between study areas. Here, we propose to take advantage of waterhole monitoring with camera traps on the Ongava Game Reserve, Namibia, to compare six population size estimators to characterize the biases associated with spatial, temporal and individual variability in detection rates. Being water dependent but with a capacity to spend several days without drinking, individual giraffes typically come to drink every two or three days (Shorrocks, 2016). This behaviour can potentially generate variation in detection probability once individuals have visited a waterhole, i.e. an individual seen on a given day will be less likely to be seen on the following day. It is also known that males and females have different behaviours and resource requirements (see Gaillard et al. (2003), for examples in different large herbivore species), therefore the frequency of waterhole visits might differ between sexes for giraffes (Shorrocks, 2016).

A practical advantage of using giraffe as a study species is that one can use its idiosyncratic coat patterns to uniquely identify individuals from photographs, and then apply CR estimators to evaluate population abundance (Brown et al., 2019; Lee et al., 2022). This biological feature offers the opportunity to quantify the impact of detection heterogeneity on population size estimates, and to assess the relevance of simpler indices of abundance to monitor giraffe (and other species) populations. We compared the abundance estimates obtained from proven CR methodologies, with *N*-mixture estimates, rarefaction curves, and raw count data by observers on the Ongava Game Reserve in 2016.

Material and Methods

Study area

Ongava Game Reserve (OGR) is located in Namibia, covering an area of approximately 300 km^2 immediately to the south of Etosha National Park with a common boundary on Ongava's north side (Fig. 1). OGR

is enclosed by electrified fences preventing movement of ungulates in and out the reserve. OGR hosts several large mammalian predators including lion (*Panthera leo*), cheetah (*Acynonyx jubatus*), leopard (*Panthera pardus*) and spotted hyena (*Crocuta crocuta*), all potential predators of juvenile or adult giraffes (Shorrocks, 2016). Hunting is prohibited on OGR and poaching of giraffes is unlikely due to a high-intensity anti-poaching presence on the reserve.
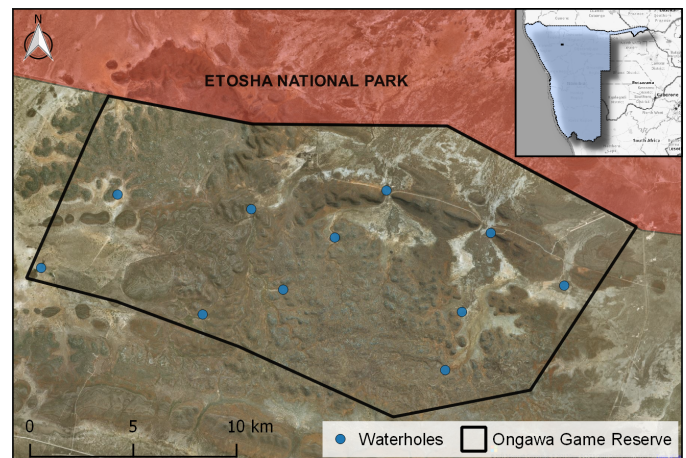

Figure 1 – Spatial distribution of waterholes surveyed in 2016 with camera traps to monitor wildlife abundance at Ongava Game Reserve, Namibia. We extracted abundance data for giraffes (*Giraffa camelopardalis angolensis*) to be applied to different estimators of giraffe population size.

The habitat is termed *Karstveld*, with vegetation primarily (*Colophospermum mopane*) shrub and woodland, with some areas savannah-like. OGR's relief is mostly dolomite hills, with a few small open plain areas and a well-defined ridge and small mountains in the central and northern part of the reserve. The weather zone for the reserve is typical for semi-arid northern Namibia, with an average annual rainfall of 380 mm (see Stratford and Stratford, 2011, for further details). There are several natural dams on the reserve, although most of these only contain water during the rainy season (January to April). During the dry season (May to December) water is only available at 12 artificial waterholes.

Count data

From the 8th to the 28th of September 2016 (a total of 21 days), between three and eight camera traps (®Reconyx RC-55 and HC-500 and ®Bushnell Trophy series) were deployed at each waterhole to monitor their usage by wildlife (see Table S1). Each camera was mounted inside a stainless-steel protection case bolted to a tree or a pole within 10–15 m of the waterhole. Reconyx cameras were set to record a sequence of 10 images with a delay of 30 seconds between sequences, while Bushnell cameras recorded sequences of 3 images with a delay of 15 seconds. We extracted all images containing giraffes and their associated metadata (date and time).

The camera traps yielded a total of 30 913 giraffe images. From these, 85 were discarded because the date and time of capture recorded by the camera were wrong. When possible, individual giraffes were manually identified in each image based on their unique coat patterns with the help of HotSpotter software (Crall et al., 2013). Whenever a giraffe could not be identified from its coat patterns or with the help of other images in the sequence, it was labelled as unknown. Where possible, we recorded the age-class (adults, sub-adults and juveniles) and sex of each individual.

Population size estimations

Capture-Recapture models

We built daily capture histories for each individual giraffe over the *t* = 21 days of the camera trap survey. We then analysed these capture histories with CR methods (Lebreton et al., 1992) in a Bayesian framework (see Kéry and Schaub, 2011). Each giraffe observation at a wa-

terhole is the product of survival (φ) and detection (p) probabilities, conditional on first observation. We implemented closed population estimators of abundance because of the fence running all around OGR, and because preliminary analyses estimated survival rate to $\varphi = 1$ from open population models. We modelled detection probability p on the logit scale as a function of time (i.e day, categorical variable with 20 levels), whether the individual was seen at any waterhole the previous day or not (categorical variable with 2 levels), and of the total number of functioning cameras (covariate). We also included random effects of the individual (σ_{id}^2) and of time (σ_t^2). Because we could not identify the sex of two individuals, we treated sex as a latent Bernouilli variable S_i of parameter π corresponding to the population sex-ratio. We then entered S_i as an explanatory variable (categorical variable with 2 levels) of p. Taken together, our set of fitted models covered the standard estimators for population size namely M_t (time effect), M_{th} (time and individual heterogeneity effects) and M_{tbh} (time, individual heterogeneity and behavioural effects: see Otis et al., 1978). In addition to these standard models, we fitted a spatially explicit model (SECR, Efford 2004) to estimate giraffe population size using the the SCRBayes R package (Royle et al., 2009), hence accounting for movement of animals between waterholes. We selected the statistically significant variables from the posterior parameter distributions and only kept variables for which 0 was excluded from the 95 % credible interval.

Rarefaction curves

We also estimated population size using the rarefaction curves method (see Petit and Valière, 2006). Rarefaction curves have been used for decades to estimate species diversity (Colwell and Coddington, 1994). Over the course of the survey, the cumulative number of different giraffes seen at waterholes (hereafter noted C_t) increased from day 1 to day 21 (see Fig. 2). Two different non-linear functions have been proposed in the literature for the case of population size estimation:

1. the hyperbolic function (Kohn et al., 1999): $C_t = \dfrac{N_s \times t}{b - t}$;

2. the exponential function (Eggert et al., 2003): $C_t = N_s \times (1 - e^{c \times t})$;

where t is time in days ranging from 1 to 21, and b and c are breakage parameters, i.e. the rate of decrease of the number of new individuals adding up in time. We therefore fitted the two functions to the cumulative number of new giraffes C_t in a Bayesian model to produce another estimate of population size (N_s). Note that this approach assumes a constant detection rate over time, space and between individuals, given by $p_s = C_{21}/N_s$ and requires individuals to be uniquely identified. We assessed the fit of the data to these models with a χ^2 goodness-of-fit (GOF) test. We hence compared the sum of the difference between fitted and expected numbers of giraffes seen per day, each squared and divided by the expected value, to a χ^2 with $t - 3$ degrees of freedom (k=two model parameters + 1) at a significance level $\alpha = 0.05$.

N-mixture models

The third population size estimator we applied was the N-mixture model (Royle, 2004). The N-mixture model assumes that repeated counts of animals in time and space are the outcome of combined probability models for the unknown population abundance (N_N) and for the detection (p_N). For population abundance, the Poisson, negative binomial and zero-inflated Poisson distributions are the most commonly used, but other discrete distributions may be considered (see below). For the detection process, a binomial distribution (with parameters N_N and p_N) accounts for undetected animals. The N-mixture model assumes a demographically closed population and an equal detection probability for all individuals. We estimated population size by fitting four N-mixture models to the giraffe data ($t = 21$ days, $s = 12$ waterholes), allowing for temporal variation in detection probabilities (Kéry et al., 2009).

We replicated the analyses of population size estimation for two data sets. The first data set consisted in the number of different and uniquely recognized giraffes seen per day at each of the 12 waterholes. We used a binomial distribution to model the observation process. Here, we considered another distribution mixture accounting for
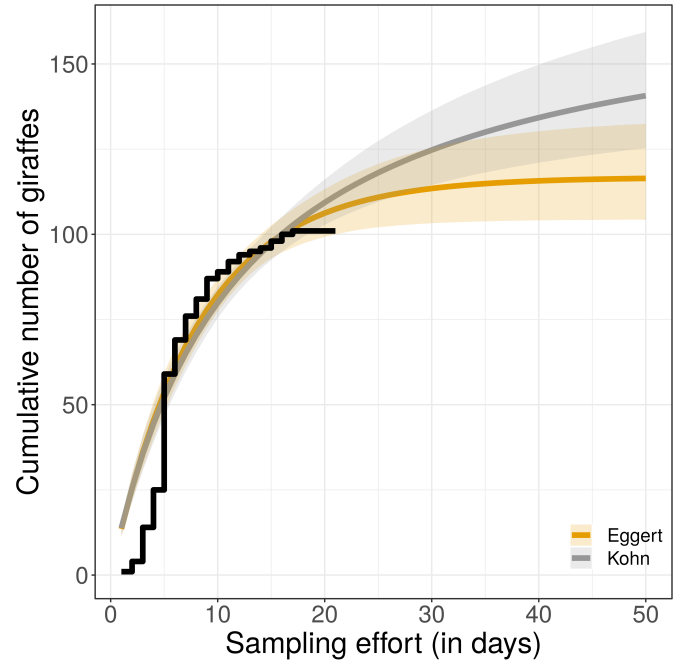

Figure 2 – Rarefaction curves for individual giraffe (*Giraffa camelopardalis angolensis*) detected during the 21-day study period in 2006 on Ongava Game Reserve, Namibia (step curve in black). Continuous lines and associated shaded areas represent predictions and 95% credible intervals of rarefaction models. We fitted two rarefaction equations proposed by Eggert et al. (2003) and Kohn et al. (1999) to the problem of population size estimation using a Bayesian framework.

the non-independence between individuals, the β-binomial–binomial N-mixture models (Martin et al., 2011). We discarded the zero inflated Poisson – binomial mixture because of its poor performance in general (Veech et al., 2016). For the second data set, we used the total number of giraffes seen (without individual recognition) and was hence more closely related to counts carried out in many reserves where individuals identification is not done. Here, we used a Poisson model for the observation process because double counts were very frequent from camera-trap photographs, resulting in a Poisson–Poisson distribution mixture (Kéry and Royle, 2020). To achieve convergence and facilitate parameter estimations, we included a temporal correlation for detection rates (first order autoregressive model, see Kéry and Royle (2020), p. 305–306). Note that in the case of Poisson – Poisson N-mixture models, we no longer estimate a detection probability ($0 < p < 1$) but a detection rate instead ($\psi > 0$).

We fitted all CR (except SECR), rarefaction and N-mixture models using JAGS 4.0 (Plummer, 2003). We used non-informative prior distributions for all estimated parameters except for N_s in the rarefaction curves models, for which we used a half-normal distribution to ensure that number of animals was > 0. We ran three Monte-Carlo (MCMC) chains, with a burn-in of 10 000 iterations before saving 5 000 iterations to get the posterior distributions of parameters at convergence. We checked convergence graphically to ensure good mixing of MCMC chains and used Gelman's h for an objective convergence criterion (convergence is reached when h is close to 1; Gelman and Pardoe, 2006). The R and JAGS code we used is freely accessible on-line at https://github.com/cbonenfant.

Results

Camera trap data set

Giraffes were recorded at 10 of the 12 waterholes surveyed. A total of 101 individuals were identified from the camera trap images: 58 adult females, 41 adult males and two juveniles of unknown sex. For all but six individuals, we obtained identification images from both sides of the animal. For five individuals, we only had images from the left side and only a front shot for the remaining animal. The majority of individuals (66 %, $n = 58$) were seen at a single waterhole, while 27 % ($n = 24$) and

7 % ($n = 6$) were seen at two and three waterholes respectively. On average, 28 unique giraffes were detected per day with camera traps, with a minimum of 8 and a maximum of 54 (median of 29.5 individuals). For 98 % of the individuals, we could assign the age-class.

Population size estimates

Capture-recapture models

From capture histories, the best model describing the observed variability in detection rate included time variation (i.e. differences in detection probability between days), sex ($\hat{\beta} = {}_{-0.60} -0.14 {}_{0.30}$), whether the individual was seen at any waterhole the day before ($\hat{\beta} = {}_{-2.95} -2.32 {}_{-1.74}$), and the first order interaction between sex and previous visit ($\hat{\beta} = {}_{0.41} 1.17 {}_{1.93}$). We detected a marked variability in daily detection probabilities over the course the of the study, ranging from $\hat{p} = {}_{0.00} 0.02 {}_{0.05}$ on day 1, to $\hat{p} = {}_{0.35} 0.47 {}_{0.59}$ on day 15. On any day, females were ${}_{0.03} 0.11 {}_{0.18}$ times less likely to be detected at any waterhole following a detection, while a male was ${}_{0.15} 0.30 {}_{0.50}$ times less likely to be detected if it was seen the day before. Once time, sex and previous visit had been accounted for, the remaining individual heterogeneity in detection rate was ($\hat{\sigma}_{id}^2 = {}_{0.40} 0.71 {}_{1.21}$). The population size estimate returned from our best model of detection rate was $\hat{N} = {}_{101} 104 {}_{109}$ individuals (Table 1). Using SECR to account for animal movement and the spatial distribution of camera traps on OGR increased the population size by 5 %, with an estimate of $\hat{N} = {}_{103} 109 {}_{115}$. Parameter estimates for the SECR models were $\hat{\sigma} = {}_{1868.92} 1981.20 {}_{2102.03}$ for scale of the half-normal distribution, corresponding to the average movement radius of giraffes, and $\hat{\lambda}_0 = {}_{0.24} 0.28 {}_{0.32}$ for the expected detection rate of an individual whose home-range centre is exactly at the trap location.

Rarefaction curve models

We calculated the cumulative number of newly detected individuals over the 21 days duration of the study (Fig. 2). The number of new individuals increased steeply up from day 1 to day 16 when it started to level off. It took 19 days to observe all the individuals identified during the study period (Fig. 2). Fitting the hyperbolic and exponential rarefaction curves to estimate population size gave contrasting results (Table 1). While the exponential equation returned a population size of ${}_{104} 117 {}_{134}$ giraffes, the hyperbolic equation projected a population size 49 % larger (${}_{145} 175 {}_{215}$). Breakage coefficients were $\hat{b} = {}_{0.09} 0.12 {}_{0.16}$ and $\hat{c} = {}_{7.9} 11.9 {}_{17.7}$ for the exponential and hyperbolic equations respectively. Overall, the fit of the two rarefaction curves to the data was poor for the exponential and hyperbolic equations (Fig. 2), with $\chi^2_{df=18} = 339.4$ and $\chi^2_{df=18} = 330.1$, both GOF tests rejected the null ($\chi^2_{df=18} = 9.39$ at the confidence level $\alpha = 0.05$). Precision of the estimates was of the same magnitude, close to 10 % for both models (Table 1).

N-mixture models

We applied three different N-mixture models to the camera trap data yielding contrasting results. The Poisson–binomial model returned an estimate of $\hat{N}_{PB} = {}_{173} 215 {}_{263}$ giraffes (Table 1), hence 80 % larger than the estimation from the best CR model. The β-binomial – binomial mixture estimated abundance to $\hat{N}_{\beta BB} = {}_{107} 124 {}_{156}$ giraffes. The associated parameters of the β-binomial function were $\hat{\alpha} = {}_{0.32} 0.44 {}_{0.58}$ and $\hat{\beta} = {}_{1.13} 1.82 {}_{2.91}$, giving a correlation $\hat{\rho} = {}_{0.22} 0.31 {}_{0.40}$. According to this model, the mean daily detection probability was $\hat{p} = {}_{0.14} 0.20 {}_{0.25}$, ranging between $\hat{p} = {}_{0.00} 0.01 {}_{0.10}$ and $\hat{p} = {}_{0.63} 0.87 {}_{0.99}$. Fitting a Poisson–Poisson N-mixture model to raw observations led to an estimated population size of $\hat{N}_{PP} = {}_{79} 87 {}_{99}$ giraffes (Table 1). The mean detection rate was $\hat{\psi} = 0.55$ but varied from $\hat{\psi}_{k,t} = {}_{0.00} 0.01 {}_{0.03}$ to $\hat{\psi}_{k,t} = {}_{1.79} 3.11 {}_{5.10}$ according to time and space. The first order temporal auto-correlation coefficient (AR(1)) was estimated as $\hat{\tau} = {}_{-1.00} -0.56 {}_{-0.03}$. Note that the Poisson-Poisson model was particularly difficult to fit to the data as we experienced many convergence issues.

Frequency of waterhole visits

We computed the mean time of return to a waterhole and frequency of visits from the daily probabilities as estimated from the CR model. To do so, we simulated 5 000 capture histories from a multinomial distribution taking the observed detection probabilities for each day as the distribution model parameters. For each capture history, we calculated the difference in days between successive visits to any waterhole, and its inverse to get the frequency of visits. The mean time of return to a waterhole of giraffe was $\hat{T}_l = {}_{1.6} 5.0 {}_{14.0}$ days for males, yielding a frequency of $\hat{f} = {}_{0.07} 0.26 {}_{0.62}$. Females tended to visit waterholes more frequently with a mean time lag of $\hat{T}_l = {}_{1.7} 4.0 {}_{9.5}$ days between two observations, and a frequency $\hat{f} = {}_{0.10} 0.30 {}_{0.58}$ over 21 days of monitoring.

Discussion

Population abundance is the core state variable of population dynamics from which the population growth rates are derived (Caughley, 1977). Our study system at OGR offers a unique opportunity to apply and compare different methods to estimating giraffes abundance. Because giraffes can be recognized from their coat patterns, we were able to apply methods based on the re-observations of individuals (capture-recapture *sensu largo*), which were then compared to other abundance estimators traditionally used in wildlife monitoring in African national parks (Jachmann, 2012). With the exception of the Poisson-binomial N-mixture model, all estimators yielded potentially acceptable results (see Table 1). In comparison to the CR estimate, the other abundance estimators deviated by −16 to +106 %. We caution against overestimating giraffes abundance when using N-mixture models or rarefaction curves at large scale and for conservation purposes. As there is marked heterogeneity in detection probability in time and among individuals, the drinking behaviour of giraffe likely accounts for the discrepancies we report among abundance estimators, and should be carefully considered for other species monitored at waterholes.

Individual variability, local habitats and the use of a plethora of available methods to estimate population abundance (Seber, 1982) have led to inconsistent ways of monitoring wild populations of large herbivores among and, sometimes, within sites. For instance, in Hwange National Park, Zimbabwe, giraffe density estimation was derived from distance sampling (Valeix et al., 2008), while in the Serengeti, Kenya, aerial counts were preferred as an index of abundance (Strauss, 2014, see also Table 2 for an overview). We show here that the choice of a particular method to estimate giraffe abundance has profound consequences on the results. On OGR, the range of estimated population sizes varied by more than two-fold, from 87 to 215, yielding densities of 0.29 and 0.71 individuals·km^{-2}. Which estimator to implement and to apply to empirical data is not trivial, and comparisons of results with well-known, reference methods is advised (e.g. Corlatti et al., 2017; Pellerin et al., 2017). In our case, and in the absence of knowledge of the true number of giraffes, we considered the population size of 104 giraffes (density of 0.34 individuals·km^{-2}) derived from CR models to be the most reliable among all estimates. CR methods are usually regarded as the gold standard because of their flexibility in dealing with detection probability and the long history of use since the publication of its principle by Petersen-Lincoln (Pollock, 1976).

While population size as estimated from Eggert's equation is somewhat close to CR models (117 vs. 104), the estimation from Kohn's equation seems biologically unrealistic and should be disregarded (see also Frantz and Roper, 2006, for similar results on simulated data). With 175 individuals, giraffe density (0.58 individuals·km^{-2}) would be almost 3 times larger than previous estimates at Etosha National Park (Table 2), neighbouring OGR with similar rainfall conditions (Fig. 1). Such a high population density should trigger density-dependent processes, first manifested by a reduction in reproduction rates of females or low juvenile survival in large herbivores (Bonenfant et al., 2009). Rarefaction curves were shown to give biased estimation of biodiversity when species are not uniformly distributed in space (Collins and Simberloff, 2009). Similarly, projecting the number of total individuals from rarefaction curves (e.g. Petit and Valière, 2006) is likely to be in-

Table 1 – Estimated population size ($\hat{N}$) of giraffe (*Giraffa camelopardalis angolensis*) at Ongava Game Reserve, Namibia, in September 2016, from the monitoring of 12 waterholes for 21 days. The capture-recapture estimator modelled detection probability of animals accounting for daily variation (t), sex of individual (*sex*), and whether the giraffe has previously visited a waterhole the day before or not (b). h stands for the individual variation in detection probability. For the sake of comparisons, we present the average detection probabilities $\overline{p}$ *a posteriori* as the number of counted animals divided by $\hat{N}$. For N-mixture models, abundance estimation used the number of uniquely identified giraffe each day at every waterhole, hence removing double counts (Poisson–binomial and β-binomial–binomial mixtures) to return population size and detection probability. Another N-mixture model used the raw number of giraffe counted at each waterhole instead (Poisson–Poisson N-mixture), which is the most common configuration in wildlife counts in Africa. In this case, the model accounts for multiple counts of the same giraffe. We report here the point estimates and associated 95% credible intervals as: $_{\text{lower limit}}$ mean $_{\text{upper limit}}$. C_v stands for the coefficient of variation of $\hat{N}$.

Abundance estimator	$\hat{N}$	$\overline{p}$	C_v
Capture-recapture p_t	$_{101}$ 101 $_{103}$	$_{0.99}$ 0.99 $_{1.00}$	1.0%
Capture-recapture p_{t+h}	$_{101}$ 103 $_{107}$	$_{0.94}$ 0.98 $_{1.00}$	1.7%
Capture-recapture $p_{t+sex+h}$	$_{101}$ 103 $_{108}$	$_{0.93}$ 0.98 $_{1.00}$	1.7%
Capture-recapture $p_{t+sex+b+h}$	$_{101}$ 104 $_{109}$	$_{0.92}$ 0.98 $_{1.00}$	2.1%
Capture-recapture $p_{t+sex+b+h}$	$_{101}$ 104 $_{110}$	$_{0.92}$ 0.97 $_{1.00}$	2.2%
Spatially explicit capture-recapture	$_{103}$ 109 $_{115}$	$_{0.87}$ 0.92 $_{0.98}$	3.1%
Rarefaction curve (Kohn)	$_{145}$ 175 $_{215}$	$_{0.47}$ 0.57 $_{0.70}$	10.0%
Rarefaction curve (Eggert)	$_{104}$ 117 $_{134}$	$_{0.75}$ 0.86 $_{0.97}$	6.3%
N-mixture (Poisson–binomial)	$_{173}$ 215 $_{263}$	$_{0.38}$ 0.47 $_{0.58}$	4.4%
N-mixture (β-binomial–binomial)	$_{107}$ 124 $_{156}$	$_{0.65}$ 0.81 $_{0.94}$	10.1%
N-mixture (Poisson–Poisson)	$_{79}$ 87 $_{99}$	$_{1.02}$ 1.16 $_{1.28}$[a]	5.4%

[a] For this N-mixture model, detection is no longer a probability but a rate that can take values > 1.

fluenced by heterogeneity in detection probability among individuals. While Kohn's equation returned a large number of giraffes compared to the CR estimate, Eggert's equation almost matched our reference population size. However, with no replication of our observations and counts, we cannot assess the robustness of Eggert's equation to heterogeneity in detection probability among individuals. All in all, the fit of the two rarefaction curves were poor (Fig. 2) making the inference on population size spurious at best, in addition to requiring individual identification of giraffes. If individual identification is to be done, we advise the use of CR methods instead of rarefaction curves to estimate giraffe abundance.

Although N-mixture models are more and more used to analyse count data, their reliability is regularly questioned (Dennis et al., 2015; Link et al., 2018; Knape et al., 2018; Nakashima, 2020). Comparisons with other proven methods such as CR are scarce, despite their value. For giraffe, the estimation of population abundance from N-mixture models suffers from either a severe overestimation (215 for the Poisson–binomial mixture) to an underestimation (87 for the Poisson–Poisson mixture) when applied on raw, unprocessed data without identification of individuals. If individual identification is not possible, double counts are likely to occur in the raw counts. Double counting therefore is a commonly encountered situation in count operations at waterholes in many African parks. A Poisson-Poisson N-mixture is the natural solution to this situation by estimating a detection rate ($\psi >$ 1) where individuals can be seen more than once. Unfortunately, our results suggest poor performance of the Poisson–Poisson N-mixture model in estimating giraffe abundance. This model produced the lowest population size estimate, being −36 % smaller than CR estimate (87 vs 119 giraffes). Despite the occurrence of frequent double counts (empirical rate: 568/119 = 4.77 from CR data), the Poisson–Poisson N-mixture model failed to estimate this quantity correctly ($\hat{\lambda} \times \hat{\psi}$ =1.06), maybe because of unmodelled heterogeneity, in addition to temporal and spatial variation in the detection probability of animals. Since most giraffes live in groups, we also faced non-independence of individual detection which, when accounted for with a β–binomial distribution in the N-mixture model (Martin et al., 2011), returns much more sensible estimates of population size (124 individuals) than any other assumed distributions of the detection process (Table 1).

A strength of CR estimators over the rarefaction curves and N-mixture models is their ability to model detection probabilities not only in time and space, but also at the individual level. An important source of heterogeneity in detection probability we observed was the frequency of visit to waterholes. Giraffe visit to waterholes is pri-

marily motivated by thirst, and if they must drink on a regular basis, they can skip drinking for several days in a row (Shorrocks, 2016). On OGR, giraffe's return frequency to waterholes was between 0.26 and 0.30 for males and females respectively (one visit every 4–5 days on average), which is lower than previously observed. For instance, Shorrocks (2016) reported a frequency of 0.61, while Caister et al. (2003) recorded daily drinking in Niger ($f \approx 1$). Such a marked difference in drinking frequency may have both biological and technical explanations. On OGR, giraffes may find enough water in forage or access to small, non-monitored water sources, making the need to visit larger but dangerous waterholes less stringent. An alternative would be that camera traps might fail to trigger in the presence of an animal, which is sensitive to camera placement, settings and performance (Rovero et al., 2013; McIntyre et al., 2020), or because the photograph was of too low quality to allow for individual identification (e.g. blurry or dark images). Independently of its cause, this behaviour generates a particular detection pattern. Once an animal has visited a waterhole to drink, it will be less likely to be detected the following days, therefore breaking the assumption of constant detectability of many abundance estimators. In CR terminology, giraffes are "trap shy" and several solutions have been proposed by statisticians to reduce bias on abundance estimates in the CR framework (Pollock, 1980).

Our study on OGR is a clear illustration that the assumption of a constant detection rate is not met, even with a fixed sampling design and a fine, daily, temporal resolution of the monitoring. Detection probability varied substantially from one day to another, ranging from 0.02 to 0.47. This result is a major warning against the use of raw (i.e. unidentified individuals) count data, such as the number of giraffes seen per day, to monitor giraffe populations in the wild (see Anderson, 2001, for a general argument). Variation in daily detection probability resulted not only from the drinking and grouping behaviour of giraffes, but also from the number of camera traps in service over the course of the study. Several cameras stopped recording pictures because of battery failure or full memory cards. A sampling design based on fixed camera traps at waterholes hence does not guarantee a constant detectability. This marked variability in detection probability in time likely accounts for the discrepancy we report among the six population abundance estimators. In practice, estimating abundance of giraffes should preferably consider methods flexible enough to account for their drinking behaviour.

Sampling large mammal populations with camera traps is of great practical advantage. When it comes to estimation of population abundance from camera-trap data, the long-standing issues of detection and

Table 2 – Reported densities of giraffe (*Giraffa camelopardalis ssp.*) populations in Africa (in number of individuals·km^{-2}). When abundance was estimated for several years, repeated lines in the same location give the range of densities recorded on the site.

Site	Ecosystem	Country	Density	Estimator	Reference
Chobe National Park	Floodplains – mixed woodland	Botswana	0.110 (–)	Aerial counts	Mcqualter (2018)
Great Rift Valley	Savannah	Kenya	0.468 (88/188)	Ground census	Muller (2019)
Great Rift Valley	Savannah	Kenya	0.405 (77/190)	Ground census	Muller (2019)
Mara Region	Open grassland	Kenya	0.750 (–)	Aerial counts	Ogutu et al. (2011)
Mara Region	Open grassland	Kenya	0.080(–)	Aerial counts	Ogutu et al. (2011)
Etosha National Park	Savannah plains / mixed savannah	Namibia	0.150(–)	Aerial counts	Brand (2007)
Etosha National Park	Savannah plains / mixed savannah	Namibia	0.200(–)	Aerial counts	Brand (2007)
Ongava	Forest savannah	Namibia	0.336 (–)	Capture-recapture	This study
Kouré and Fandou Plateaus	Forest savannah	Niger	0.241 (–)	Census (photo ID)	Suraud et al. (2012)
Lake Manyara National Park	Evergreen groundwater forests	Tanzania	0.570 (0.570-0.580)	Distance sampling	Kiffner et al. (2020)
Lake Manyara National Park	Evergreen groundwater forests	Tanzania	1.210 (1.180-1.25)	Distance sampling	Kiffner et al. (2020)
Mkomazi National Park	Savannah-woodland ecosystem	Tanzania	1.165 (0.808)	Distance sampling	Mseja et al. (2020)
Tarangire Ecosystem	Savannah-woodland ecosystem	Tanzania	0.791 (0.073)	Capture-recapture	Lee & Bond (2016)
Tarangire Ecosystem	Savannah-woodland ecosystem	Tanzania	1.202 (0.760)	Capture-recapture	Lee & Bond (2016)
Tarangire Ecosystem	Savannah-woodland ecosystem	Tanzania	0.173 (0.057)	Capture-recapture	Lee & Bond (2016)
Saadani National Park	Savannah-forest mosaic	Tanzania	0.106-1.400	Distance sampling	Treydte et al. (2005)
Serengeti	Scrub thicket-open grassland	Tanzania	0.18-2.59	Aerial counts	Strauss (2014)
Shamwari ecosystems	Savannah-forest mosaic	South Africa	0.744 (–)	Walked transects	Hayward et al. (2007)
Lupande	Mopane/miombo woodlands	Zambia	1.274 (930/730)	Double counts (aerial)	Jachmann (2002)
Hwange National Park	Forest savannah	Zimbabwe	0.170 (–)	Distance sampling	Valeix et al. (2008)
Gonarezhou National Park	Dry deciduous savannah	Zimbabwe	0.470 (0.140)	Distance sampling	Ndiweni et al. (2015)
Malipati Sarafi Area	Dry deciduous savannah	Zimbabwe	0.010 (0.030)	Distance sampling	Ndiweni et al. (2015)

the modelling of its heterogeneity in time, space and among individuals still apply. We found the deviation of *N*-mixture and rarefaction curve models from our reference CR estimation deteriorated when the data are not processed using individual identification. For species with unique coat patterns, individual identification with machine learning and artificial intelligence is now robust, efficient, and is becoming more easily available and less of an obstacle for wildlife managers (see Miele et al., 2021). This may apply to other African species of large herbivores such as zebras sp., greater (*Tragelaphus strepsiceros*) and lesser kudu (*T. imberbis*), wildebeest (*Connochaetes taurinus*) or bushbuck (*Tragelaphus scriptus*) that all bear idiosyncratic marks. We believe the gain in accuracy in population abundance estimation is worth the time allocated to it and will serve the conservation of such species. 🖎

References

Anderson D.R., 2001. The need to get the basics right in wildlife field studies. Wildl. Soc. Bull. 29:1294–1297.

Apollonio M., Putman R., Grignolio S., Bartoš L., 2010. Hunting seasons in relation to biological breeding seasons and the implications for the control or regulation of ungulate populations. In: Putman R., Apollonio M., Andersen R. (Eds.) Ungulate management in Europe, Cambridge University Press, 80–105.

Bonenfant C., Gaillard J.M., Coulson T., Festa-Bianchet M., Loison A., Garel M., Loe L.E., Blanchard P., Pettorelli N., Owen-Smith N., Du Toit J., Duncan P., 2009. Empirical evidence of density-dependence in populations of large herbivores. Adv. Ecol. Res. 41:313–357.

Brand R., 2007. Evolutionary ecology of giraffes (*Giraffa camelopardalis*) in Etosha National Park, Namibia. Ph.D. thesis, Newcastle University.

Brown M.B., Bolger D.T., Fennessy J., 2019. All the eggs in one basket: a countrywide assessment of current and historical giraffe population distribution in Uganda. Global Ecol. Conserv. 19:e00612.

Buckland S., Goudie I., Borchers D., 2000. Wildlife population assessment: past developments and future directions. Biometrics 65:1–12.

Burnham K.P., Anderson D.R., Laake J.L., 1980. Estimation of density from line transect sampling of biological populations. Wild. Monogr. 72:3–202.

Burton A.C., Neilson E., Moreira D., Ladle A., Steenweg R., Fisher J.T., Bayne E., Boutin S., 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. 52(3):675–685.

Caister L.E., Shields W.M., Gosser A., 2003. Female tannin avoidance: a possible explanation for habitat and dietary segregation of giraffes (*Giraffa camelopardalis peralta*) in Niger. Afr. J. Ecol. 41(3):201–210.

Caughley G., 1977. Analysis of vertebrate populations. Wiley, London.

Choquenot D., 1995. Assessing visibility bias associated with helicopter counts of feral pigs in Australia's semi-arid rangelands. Wildl. Res. 22(5):569–577.

Collier B.A., Ditchkoff S.S., Raglin J.B., Smith J.M., 2007. Detection probability and sources of variation in white-tailed deer spotlight surveys. J. Wildl. Manag. 71(1):277–281.

Collins M.D., Simberloff D., 2009. Rarefaction and nonrandom spatial dispersion patterns. Environ. Ecol. Stat. 16(1):89–103.

Colwell R.K., Coddington J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 345(1311):101–118.

Corlatti L., Nelli L., Bertolini M., Zibordi F., Pedrotti L., 2017. A comparison of four different methods to estimate population size of Alpine marmot (*Marmota marmota*). Hystrix 28(1):61–67.

Crall J.P., Stewart C.V., Berger-Wolf T.Y., Rubenstein D.I., Sundaresan S.R., 2013. Hotspotter–patterned species instance recognition. In: 2013 IEEE workshop on applications of computer vision (WACV), 230–237.

Dail D., Madsen L., 2011. Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67(2):577–587.

Dennis E.B., Morgan B.J., Ridout M.S., 2015. Computational aspects of *N*−mixture models. Biometrics 71(1):237–246.

Duckworth J., 1998. The difficulty of estimating population densities of nocturnal forest mammals from transect counts of animals. J. Zool. 246(4):443–486.

Efford M., 2004. Density estimation in live-trapping studies. Oikos 106(3):598–610.

Eggert L., Eggert J., Woodruff D., 2003. Estimating population sizes for elusive animals: the forest elephants of Kakum National Park, Ghana. Mol. Ecol. 12(6):1389–1402.

Elenga G., Bonenfant C., Péron G., 2020. Distance sampling of duikers in the rainforest: Dealing with transect avoidance. PLoS One 15(10):e0240049.

Frantz A.C., Roper T.J., 2006. Simulations to assess the performance of different rarefaction methods in estimating population size using small datasets. Conserv. Genet. 7(2):315–318.

Gaillard J.M., Loison A., Toïgo C., 2003. Variation in life history traits and realistic population models for wildlife management. In: Festa-Bianchet M., Apollonio M. (Eds.) Animal behaviour and wildlife conservation, Island Press, 115–132.

Gelman A., Pardoe I., 2006. Bayesian measures of explained variance and pooling in multilevel (hierarchical) models. Technometrics 48:241–252.

Gilbert N.A., Clare J.D., Stenglein J.L., Zuckerberg B., 2021. Abundance estimation of unmarked animals based on camera-trap data. Conserv. Biol. 35(1):88–100.

Hamel S., Killengreen S.T., Henden J.A., Eide N.E., Roed-Eriksen L., Ims R.A., Yoccoz N.G., 2013. Towards good practice guidance in using camera-traps in ecology: influence of sampling design on validity of ecological inferences. Methods Ecol. Evol. 4(2):105–113.

Hayward M.W., O'Brien J., Kerley G.I., 2007. Carrying capacity of large African predators: predictions and tests. Biol. Conserv. 139(1-2):219–229.

Jachmann H., 2002. Comparison of aerial counts with ground counts for large African herbivores. J. Appl. Ecol. 39(5):841–852.

Jachmann H., 2012. Estimating abundance of African wildlife: An aid to adaptive management. Springer Science & Business Media.

Jackson R.M., Roe J.D., Wangchuk R., Hunter D.O., 2006. Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildl. Soc. Bull. 34(3):772–781.

Karanth K.U., Nichols J.D., 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–5862.

Kéry M., 2018. Identifiability in N-mixture models: A large-scale screening test with bird data. Ecology 99(2):281–288.

Kéry M., Schaub M., 2011. Bayesian population analysis using WinBUGS: A hierarchical perspective. Academic Press.

Kéry M., Royle J.A., 2020. Applied hierarchical modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 2: Dynamic and advanced models. Academic Press.

Kéry M., Royle J.A., Plattner M., Dorazio R.M., 2009. Species richness and occupancy estimation in communities subject to temporary emigration. Ecology 90(5):1279–1290.

Kiffner C., Binzen G., Cunningham L., Jones M., Spruiell F., Kioko J., 2020. Wildlife population trends as indicators of protected area effectiveness in northern Tanzania. Ecol. Indic. 110:105903.

Knape J., Arlt D., Barraquand F., Berg Å., Chevalier M., Pärt T., Ruete A., Zmihorski· M., 2018. Sensitivity of binomial $N-$mixture models to overdispersion: The importance of assessing model fit. Methods Ecol. Evol. 9(10):2102–2114.

Kohn M.H., York E.C., Kamradt D.A., Haught G., Sauvajot R.M., Wayne R.K., 1999. Estimating population size by genotyping faeces. Proc. R. Soc. Lond. B Biol. Sci. 266(1420):657–663.

Le Cœur C., Thibault M., Pisanu B., Thibault S., Chapuis J.L., Baudry E., 2015. Temporally fluctuating selection on a personality trait in a wild rodent population. Behav. Ecol. 26(5):1285–1291.

Lebreton J.D., Burnham K.P., Clobert J., Anderson D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecol. Monogr. 62:67–118.

Lee D.E., Bond M.L., 2016. Precision, accuracy, and costs of survey methods for giraffe *Giraffa camelopardalis*. J. Mammal. 97(3):940–948.

Lee D.E., Lohay G.G., Cavener D.R., Bond M.L., 2022. Using spot pattern recognition to examine population biology, evolutionary ecology, sociality, and movements of giraffes: A 70-year retrospective. Mamm. Biol. 1–17.

Leslie P., Davis D., 1939. An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 94–113.

Link W.A., Schofield M.R., Barker R.J., Sauer J.R., 2018. On the robustness of N-mixture models. Ecology 99(7):1547–1551.

Martin J., Royle J.A., Mackenzie D.I., Edwards H.H., Kery M., Gardner B., 2011. Accounting for non-independent detection when estimating abundance of organisms with a Bayesian approach. Methods Ecol. Evol. 2(6):595–601.

McIntyre T., Majelantle T., Slip D., Harcourt R., 2020. Quantifying imperfect camera-trap detection probabilities: implications for density modelling. Wildl. Res. 47(2):177–185.

McQualter K.N., 2018. The ecology and behaviour of giraffe in Northern Botswana. Ph.D. thesis, University of New South Wales, Australia.

Miele V., Dussert G., Spataro B., Chamaillé-Jammes S., Allainé D., Bonenfant C., 2021. Revisiting animal photo-identification using deep metric learning and network analysis. Methods Ecol. Evol. 12(5):863–873.

Morellet N., Gaillard J.M., Hewison A.J.M., Ballon P., Boscardin Y., Duncan P., Klein F., Maillard D., 2007. Indicators of ecological change: New tools for managing populations of large herbivores. J. Appl. Ecol. 44:634–643.

Mseja G.A., Kisingo A.W., Stephan E., Martin E.H., 2020. Dry season wildlife census in Mkomazi National Park, 2015. In: Durrant J., Martin E., Melubo K., Jensen R., Hadfield L., Hardin P., L W. (Eds.) Protected areas in Northern Tanzania–Local communities, land use change, and management challenges, Springer, 133–143.

Muller Z., 2019. Rothschild's giraffe *Giraffa camelopardalis rothschildi* (Linnaeus, 1758) in East Africa: A review of population trends, taxonomy and conservation status. Afr. J. Ecol. 57(1):20–30.

Nakashima Y., 2020. Potentiality and limitations of N-mixture and Royle-Nichols models to estimate animal abundance based on noninstantaneous point surveys. Popul. Ecol. 62(1):151–157.

Ndiweni T., Zisadza-Gandiwa P., Ncube H., Mashapa C., Gandiwa E., 2015. Vigilance behavior and population density of common large herbivores in a southern African savanna. J. Anim. Plant. Sci. 25(3):876–883.

O'Connell A., Karanth K., Nichols J.D., 2011. Camera traps in animal ecology. Springer Japan, Tokyo.

O'Connor D., Stacy-Dawes J., Muneza A., Fennessy J., Gobush K., Chase M.J., Brown M.B., Bracis C., Elkan P., Zaberirou A.R.M., 2019. Updated geographic range maps for giraffe, *Giraffa spp.*, throughout sub-Saharan Africa, and implications of changing distributions for conservation. Mammal. Rev. 49(4):285–299.

Ogutu J.O., Owen-Smith N., Piepho H.P., Said M.Y., 2011. Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. J. Zool. 285(2):99–109.

Otis D.L., Burnham K.P., White G.C., Anderson D.R., 1978. Statistical inference from capture data on closed animals populations. Wildl. Monogr. 62:1–133.

Pellerin M., Bessière A., Maillard D., Capron G., Gaillard J.M., Michallet J., Bonenfant C., 2017. Saving time and money by using diurnal vehicle counts to monitor roe deer abundance. Wildl. Biol. 2017: wlb.00274.

Petit E., Valière N., 2006. Estimating population size with noninvasive capture-mark-recapture data. Conserv. Biol. 20:1062–1073.

Plummer M., 2003. JAGS: A program for analysis of bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd international workshop on distributed statistical computing, Vienna, Austria., vol. 124, 1–10.

Pollock K.H., 1976. Building models of capture-recapture experiments. J. R. Stat. Soc. Series D Stat. 25(4):253–259.

Pollock K.H., 1980. Capture-recapture models: A review of current methods, assumptions and experimental design. Stud. Avian Biol. 6: 426–435.

Rovero F., Zimmermann F., Berzi D., Meek P., 2013."Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. Hystrix 24(2):148–156.

Royle J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60(1):108–115.

Royle J.A., Karanth K.U., Gopalaswamy A.M., Kumar N.S., 2009. Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. Ecology 90(11):3233–3244.

Schwarz C., Seber G.A.F., 1999. A review of estimating animal abundance III. Stat. Sci. 14:427–456.

Seber G.A.F., 1982. The estimation of animal abundance and related parameters. C. Griffin and Co. Ltd., London, 2nd edn.

Shorrocks B., 2016. The giraffe: biology, ecology, evolution and behaviour. John Wiley & Sons.

Strandgaard H., 1967. Reliability of the Petersen method tested on a roe-deer population. J. Wildl. Manag. 31:643–651.

Strandgaard H., 1972. The roe deer (*Capreolus capreolus*) population at Kälo and the factors regulating its size. Dan. Rev. Game Biol. 7:1–205.

Stratford K.J., Stratford S.M., 2011. Fine-scale movements and use of space by spotted hyaena (*Crocuta crocuta*) on Ongava Game Reserve, Namibia. Afr. J. Ecol. 49(3):343–352.

Strauss M.K.L., 2014. Ecological and anthropogenic drivers of giraffe (*Giraffa camelopardalis tippelskirchi*) population dynamics in the Serengeti. Ph.D. thesis, University of Minnesota.

Suraud J.P., Fennessy J., Bonnaud E., Issa A., Fritz H., Gaillard J.M., 2012. Higher than expected growth rate of the endangered West African giraffe *Giraffa camelopardalis peralta*: a successful human–wildlife cohabitation. Oryx 46(4):577–583.

Swanson A., Kosmala M., Lintott C., Simpson R., Smith A., Packer C., 2015. Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. Sci. Data 2(1):1–14.

Treydte A.C., Edwards P.J., Suter W., 2005. Shifts in native ungulate communities on a former cattle ranch in Tanzania. Afr. J. Ecol. 43(4):302–311.

Trolliet F., Vermeulen C., Huynen M.C., Hambuckers A., 2014. Use of camera traps for wildlife studies: A review. Biotechnol. Agron. Soc. Environ. 18(3):446–454.

Valeix M., Fritz H., Chamaillé-Jammes S., Bourgarel M., Murindagomo F., 2008. Fluctuations in abundance of large herbivore populations: Insights into the influence of dry season rainfall and elephant numbers from long-term data. Anim. Conserv. 11(5):391–400.

Veech J.A., Ott J.R., Troy J.R., 2016. Intrinsic heterogeneity in detection probability and its effect on N-mixture models. Methods Ecol. Evol. 7(9):1019–1028.

Wearn O.R., Glover-Kapfer P., 2019. Snap happy: Camera traps are an effective sampling tool when compared with alternative methods. R. Soc. Open Sci. 6(3):181748.

Zett T., Stratford K.J., Weise F.J., 2022. Inter-observer variance and agreement of wildlife information extracted from camera trap images. Biodivers. Conserv. 31:3019–3037.

Associate Editor: F. Rovero