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Deriving observation distances for camera trap distance sampling

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Abstract

Camera trap distance sampling (CTDS)o is a recently developed survey method to estimate animal abundance from camera trap data for unmarked populations. It requires the estimation of camera-animal observation distances, which previously was done by comparing animal positions to reference labels at predefined intervals. Here, we test a photogrammetry approach to derive camera-animal observation distances. We applied both, the reference label and photogrammetry approaches to five ungulate species varying widely in body size (*Giraffa camelopardalis*, *Equus grevyi*, *Oryx dammah*, *Kobus megaceros* and *Eudorcas thomsonii*) and one ground-dwelling bird species (*Numida meleagris*) inhabiting a large enclosure and estimated their density with CTDS. Both procedures provided highly correlated observation distances ($\rho = 0.99$, $p < 0.001$). A paired t test revealed a minor but significantly higher mean of the photogrammetry approach (MD = 0.28 m, $p < 0.001$). This, however, seems negligible as for analyses, distances were grouped in intervals of 2 to 5 metres. In general, estimated animal abundance was close to the true number of individuals in the enclosure for both approaches, with the exception of zebra, whose density was underestimated. The photogrammetry approach offers an alternative approach for deriving camera-animal observation distances and is particularly useful for application in open habitats, with little occlusion of animals.

KEYWORDS
abundance, animal observation distance, camera trapping, density, distance sampling, photogrammetry

Résumé

Le distance sampling par piège photographique (Camera trap distance sampling ou CTDS en anglais) est une technique de recensement développée récemment qui permet d'estimer l'effectif de populations animales non marquées avec des pièges photographiques. Cette technique requiert l'estimation de la distance entre le piège photographique et l'animal observé, ce qui était précédemment obtenu en comparant la position de l'animal à des points de référence placés à des intervalles prédéfinis. Ici nous testons une approche de photogrammétrie pour estimer les distances entre les pièges photographiques et les animaux observés. Nous avons appliqué les deux approches, points de référence et photogrammétries, à cinq espèces d'ongulés de tailles différentes (*Giraffa camelopardalis*, *Equus grevyi*, *Oryx dammah*, *Kobus megaceros* et *Eudorcas thomsonii*) ainsi qu'une espèce d'oiseau (*Numida meleagris*) vivant dans un espace clôturé et avons estimé leur densités de populations avec le CTDS. Les deux méthodes ont fourni des distances d'observations fortement corrélées ($\rho = 0.99$, $p < 0.001$). Un t-test jumelé a révélé une moyenne légèrement plus élevée et significative pour la technique de photogrammétrie ($MD = 0.28$ m, $p < 0.001$). Celle-ci est néanmoins négligeable dans la mesure où, pour les analyses, les distances étaient groupées dans des intervalles allant de 2 à 5 mètres. En règle générale, les estimations d'abondances étaient proche du nombre réel d'individus dans l'enclos, et ce pour les deux techniques, avec l'exception des zèbres pour lesquels les densités étaient sous-estimées. La technique de photogrammétrie offre une alternative pour dériver les distances entre les pièges photographiques et les animaux observés et pourrait être particulièrement utile dans des habitats ouverts où les animaux sont peu cachés.

1 | INTRODUCTION

Remote motion-sensitive photography using camera traps (CTs) is a widely used tool for conservation and ecological studies of terrestrial vertebrates (Fleming et al., 2014; O'Connell et al., 2011). CTs allow researchers to collect data with limited interference with animals and provide information on abundance, behaviour, species richness or population dynamics (Burton et al., 2015; Caravaggi et al., 2017; O'Connell et al., 2011; Rowcliffe & Carbone, 2008). They enable standardised 24/7 data collection for long periods of time and improve the monitoring of elusive species that tend to avoid human observers. Moreover, CT data allows for comparability and replicability as observations are stored as visual information. Since many studies of biological populations require estimates of population density ($\hat{D}$), estimating $\hat{D}$ from CT data is a substantial advancement in ecological studies (Gilbert et al., 2020). If individuals within a population are clearly recognisable, for example for felids, spatially explicit capture-recapture models (SECR) can be used to calculate density (Efford et al., 2009). However, for most of the remaining species, such as ungulates, rodents or ground-dwelling birds, it is difficult to identify individuals from CT data.

In recent years, many efforts were made to develop techniques to estimate abundance of unmarked populations from CTs (Gilbert et al., 2020), including site-structured models such as the Royle-Nichols (RN) model (Royle & Nichols, 2003) or N-mixture models (Royle et al., 2004), unmarked spatial capture–recapture (USCR) models (Chandler & Royle, 2013; Royle et al., 2014), the random encounter model (REM) (Rowcliffe et al., 2008) and the random encounter and staying time (REST) model (Nakashima et al., 2018), as well as time-to-event (TTE), space-to-event (STE) and the instantaneous sampling (IS) models by Moeller et al. (2018). A detailed review of the different analytical approaches as well as their advantages and challenges is provided by Gilbert et al. (2020).

In 2017, Howe et al. developed a novel approach to estimate population density for unmarked populations by extending the well-developed and widely applied distance sampling framework (Buckland et al., 2001, 2004) to CT data. Distance sampling allows researchers to correct for imperfect detection within the area under observation (Buckland et al., 2001). Here, observation distances to animals are recorded and the distribution of these distances is used to fit a detection function $g(x)$ and to estimate the probability of an animal being detected within a certain distance from a point or line (Buckland et al., 2001), which can then be used to calculate density ($\hat{D}$) (Buckland et al., 2004).

For the successful implementation of CTDS, it is important to apply the methodology properly and to meet the basic assumptions of distance sampling. This concerns both the assumptions of detecting animals at their initial location prior to movement and the correct measurement of animal observation distances. In contrast to traditional distance sampling in which a human observer records a single distance to a detected animal, in CTDS, the camera traps usually make multiple recordings of an observed individual, either by a series of still images or by a video clip. It is, however, problematic to only take the first image or video frame upon initial detection as equivalent to a single observation in traditional distance sampling, because they are expected to be positively biased towards larger distances (Howe et al., 2017). For example, an animal approaching the CT from the distance would only be recorded once they enter the detection range, but will not be recorded close to the camera. Additionally, triggering delays may lead to animals at shorter distances having already left the narrow area close to the camera before being recorded. Howe et al. (2017) therefore proposed to use a series of snapshot moments at predefined time intervals t to ensure that times where distances are recorded are independent of triggering times. This can either be achieved by extracting snapshots at t in video recordings when using the trigger mode or by setting the CT to the time-lapse mode with interval *t*. The latter approach may be particularly useful when studying poikilothermic and small animals that are less likely to trigger the passive infrared (PIR) sensor of the camera (Bluett & Cosentino, 2013; Collett & Fisher, 2017; Pagnucco et al., 2011; Welbourne et al., 2019). Moreover, it avoids any bias and uncertainty associated with the sensor, trigger speed and recovery time of the camera, which would be expected to occur with motion-sensitive photography.

More importantly, CTDS requires alternative approaches to measure animal observation distances as they cannot be measured anymore in combination with the animal observation as in traditional distance sampling. Howe et al. (2017) suggested an approach, for which reference videos or pictures with marked localities in the area covered by the camera are to be recorded, for example at 1-metre intervals (1–15 m) (hereby referred to as reference approach). Yet, this approach is very time intensive and estimates could be prone to observer bias. Alternatively, animal observation distances may be extracted from synchronised recordings of paired cameras (Mrovlje & Vrani, 2008; Tjandranegara, 2005) or by applying photogrammetric methods to infer observation distance based on body size (Breuer et al., 2007; Shrader et al., 2006).

Given the scarcity of studies applying CTDS to date and the potential for extending the original methodology proposed by Howe et al. (2017), we were interested in (1) generating animal observation data using time-lapse photography, (2) comparing animal observation distances derived by photogrammetric methods and the reference approach described by Howe et al. (2017) and (3) to use CTDS to estimate animal abundances of different species in a large enclosure with the two approaches.

2 | MATERIAL AND METHODS

2.1 | Survey design

We placed eight camera traps (Reconyx Hyperfire HC600) in an outdoor savannah enclosure at the Zoo Leipzig, Germany, for a total of 19 days. The enclosure covers an area of roughly 11,400 m^2. Cameras were placed randomly throughout the area, yet most had to be placed at the edge of the enclosure where they could be properly mounted (Figure S1 for a map of CT positions).

All cameras were set to time-lapse mode and to record one picture every minute starting at 9:00 a.m. until 5:59 p.m. During that time, all animals were assumed to be within the enclosure. During CT installation, however, the motion sensor of the cameras was activated to record reference pictures in which we labelled 1-metre intervals between 1 and 15 m by holding up paper sheets with the respective distances printed on them. For the photogrammetry approach, we also took pictures (1–15 m) of a person holding up either a DIN A4 paper sheet (30 cm length) or a 50x50 cm cardboard.

Animals within the enclosure included Grevy's zebra (*Equus grevyi*), Nile lechwe (*Kobus megaceros*), scimitar oryx (*Orxy dammah*), Thomson's gazelle (*Eudorcas thomsonii*), Rothschild's giraffe (*Giraffa camelopardalis rothschildi*) and helmeted guineafowls (*Numida meleagris*). Animals ranged in body size (shoulder height) from 20.3 cm (helmeted guineafowl) to 350 cm (Rothschild's giraffe) (Table S1).

2.2 | Deriving animal observation distances

We obtained animal observation distances between the camera and every individual on a picture using two different approaches. First, for the reference approach, we compared pictures visually to reference pictures taken during deployment and assigned animal locations to the respective distance intervals as proposed by Howe et al. (2017). Estimated distances were rounded to the nearest 50 cm.

Second, for the photogrammetry approach, we derived distances using a common image processing software (ImageJ). Since the actual size of the reference marker (as described in 2.1) and the distance from the camera are known, we can calculate the focal length (f) of the cameras by measuring the pixel size of either the paper sheet, the cardboard or the person (Breuer et al., 2007; Shrader et al., 2006). Focal length was estimated by

$$f = d * \frac{x}{X} \tag{1}$$

where d is the horizontal distance from the camera to the reference object, x is the pixel size of the object on the picture, and X is the actual size of the object.

Measurements were conducted with the measuring function of the program ImageJ (Schneider et al., 2012). We calculated the focal length (f) for every picture (Eq. 1) and derived the mean as the focal length of that specific camera model. We assumed f to be consistent between different cameras of the same model. The formula can then be adjusted to calculate the distance of an object to the camera, if object size, for example shoulder height of the respective animal, is known.

$$d = X * \frac{f}{x} \tag{2}$$

Here, x and X refer to the measured pixel size and the actual size of the animal respectively. Distances were estimated in metres with a precision of two decimal places.

We obtained size data for the corresponding animals from literature (Kingdon, 2007; Sinclair & Ryan, 2010) (Table S1). If a size range was given, we calculated the mean to keep the error as small as possible. We also derived size metrics for different body parts (e.g. knee height) to account for pictures where the animal was not fully visible. Where both measures were available, we tested the ranks of distances derived from the two distance measurement approaches with Spearman's rank-order correlation tests and performed a paired t test on the differences of means using RStudio (RStudio Team, 2016).

Distances for the photogrammetry approach were measured up to 30 metres, because we assumed estimation of further distances to be less accurate than nearer distances and wanted to reduce errors as much as possible. During deployment, we were unable to record reference imagery at all camera locations up to 15 metres, because the PIR sensor of some cameras failed to trigger at farther distances, making it impossible to estimate observation distances up to 15 metres for every location. Because of this and because measuring distances via photogrammetry closer than 3 metres has proven difficult, we decided to also obtain a combined distance measure for the CTDS analysis, where we used either the mean of the reference and photogrammetry approach distance or the one that was available. The combined distance data set therefore included all observation of an animal within 0 and 30 metres in front of the camera.

2.3 | Estimating population size

We calculated the number of individuals following the approach of Howe et al. (2017) in which a CT is deployed at point *k* for a period of time T_k. If a set of snapshot moments is defined within T_k, *t* units of time apart, at which an image of an animal could be obtained, the temporal effort at point *k* can be defined as T_k/t. Since we programmed cameras on time-lapse mode and recorded one picture every minute independent of animal movement, the temporal effort was equivalent to the number of minutes cameras were operating (T_k). Additionally, in CTDS, it must be considered that CTs only cover a fraction of a whole circle ($\theta/2\pi°$) with θ being the horizontal angle of view (AOV) of the camera in radians, which can be obtained by manufacturer information. The AOV of the Reconyx Hyperfire HC600 cameras used in this study is 40° yielding a covered fraction of 0.11.

By making use of the distance sampling formula for point transects, population density ($\hat{D}$) can then be calculated as

$$\hat{D} = \frac{2\sum_{k=1}^{K} n_k}{\theta w^2 \sum_{k=1}^{K} T_k \hat{P}_k} \tag{3}$$

where *w* is the truncation distance beyond which observations are discarded, n_k is the number of animals recorded at point *k*, and $\hat{P}_k$ is the probability at each snapshot moment that a random animal within the survey area is detected between 0 and *w* in front of the camera.

To estimate $\hat{P}_k$, we derived the observation distance r_i for each animal present in each of the pictures with the two above-mentioned methods and fitted a detection function *g(x)* to the observed distances (Buckland et al., 2001). No distances to lying or resting animals were recorded to prevent bias from overdispersion of distance data and to avoid disproportionate effects on the shape of the detection function (Howe et al., 2017). If an animal remained in view for more than three minutes without moving considerably, it was assumed to be resting and distance recording was ceased. Since the animals in the zoo are within an enclosure of known area *a*, we can also obtain estimates of population size ($\hat{N}$).

2.4 | Analysis

To avoid underestimation of density, we corrected for limited availability, as suggested by Howe et al. (2017), because animals were not always available for detection, for example when they were resting. Moreover, smaller animals were able to leave the enclosure into the adjacent enclosure or return to their stable during feeding. We therefore included an availability factor representing the percentage of time animals were available for the detection in the denominator of the CTDS equation (Equation 3).

The availability factor for each species was calculated in two ways. First, we estimated it manually by dividing the sum of all observation by the product of the number of observations within an one-hour interval at peak activity and the number of hours cameras were operating (Cappelle et al., 2019). The second approach was to estimate the availability factor following the approach of Rowcliffe et al. (2014) using the R package *activity*. Here, the activity level (equal to availability) is calculated by fitting a flexible circular probability density function to the time of day data obtained from the observations. The proportion of time spent active (activity level) then refers to the integral under the activity function. The activity function can be further adjusted by different bandwidth values, describing the smoothing factor, to increase the function fit. Both methods rely on the assumption that all animals were available for detection at peak activity.

Density and population size estimates were derived using the software Distance 7.3 (Thomas et al., 2010). We applied a conventional distance sampling approach without any additional covariates using a point transect model with the fraction covered by the camera less than 1. The temporal survey effort was defined as the number of snapshot moments and because we took one picture per minute, equalled the number of minutes cameras were operating. For all but one camera effort was defined as 540 minutes per day that was processed. One camera was erroneously programmed to only record pictures from 9 to 9:59 a.m. and from 12 to 5:59 p.m., resulting in a reduced temporal effort of 420, which was adjusted accordingly. For the analysis, the distance data were grouped into intervals of 2 metres (for a truncation distance of 10 metres) or 3 metres (for a truncation distance of 15 metres). Between 15 and 30 metres, observations were grouped into 5-metre intervals. We included the sampling fraction (fraction of the circle covered by the camera) and the availability factor of the respective species as additional multipliers (divisors) in the model.

For the detection function, we assumed a uniform key function with a maximum of one cosine adjustment term. The field of view within the enclosure was mostly open, and there was no reason to expect a considerable decline in detection probability with increasing distance. Additionally, because cameras were not triggered by motion or PIR sensors, animals could be recorded at larger distances than would be expected when triggered. Analyses were performed for the distances derived with the reference and photogrammetry approach as well as the combined distance data set. The truncation

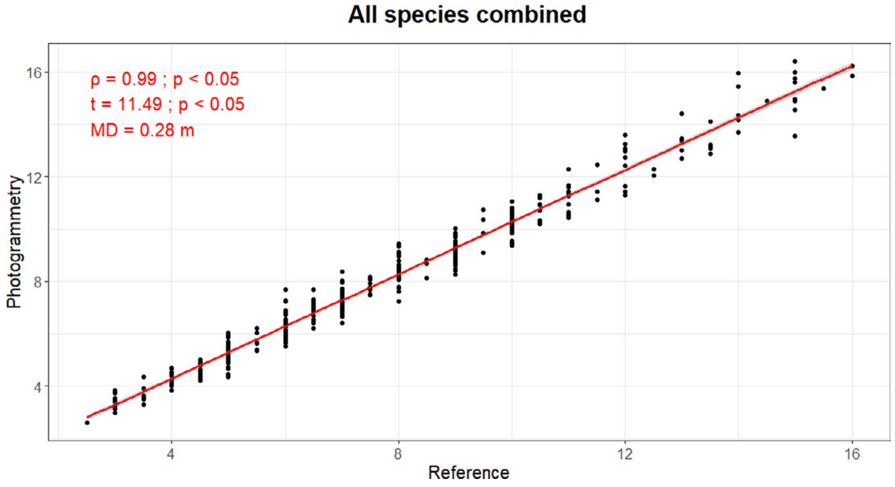

FIGURE 1 Comparison between distances derived from the reference and the photogrammetry approach. Distances derived via photogrammetry against distances visually obtained from reference pictures for all species combined (Figure S4 Supplemental material for individual figures per species). ρ, Spearman's rank correlation coefficient, t, paired t test value, MD, difference in means, $n = 369$. Dashed line indicates expected relationship (equal values for distances obtained from reference imagery and photogrammetry)

TABLE 1 Estimated availability for each species. Availability (activity level) calculated from the time of day data obtained from observations either manually or with the R package *activity* (Rowcliffe et al., 2014) using a bandwidth of 0.8 and 1 (Figure S3 Supplemental material for activity plots). 95% Confidence intervals obtained from bootstrapping (99 iterations)

Species	Activity manual	Activity R(0.8)	Activity R(1)
Kobus megaceros	0.62	0.51 [0.42, 0.53]	0.61 [0.57, 0.70]
Orxy dammah	0.82	0.75 [0.57, 0.75]	0.82 [0.71, 0.87]
Eudorcas thomsonii	0.61	0.59 [0.45, 0.60]	0.72 [0.61, 0.75]
Equus grevyi	0.60	0.59 [0.45, 0.60]	0.71 [0.62, 0.74]
Giraffa camelopardalis	0.72	0.67 [0.52, 0.72]	0.74 [0.65, 0.81]
Numida meleagris	0.56	0.51 [0.40, 0.56]	0.58 [0.50, 0.67]

distances ranged between the maximum distance obtained from the reference approach for the respective species and 30 metres.

Depending on the selected time interval of snapshot moments, observations in CTDS are non-independent. Although we selected a larger t in our study than previous studies did, that is $t = 60$ s vs. 2 s, observations were likely non-independent. Therefore, we used non-parametric bootstrapping with 999 iterations generated by sampling with replacement from the obtained data to achieve more robust estimates and to calculate 95% confidence intervals (Buckland et al., 2001). Because the non-independence of observations also introduces overdispersion causing AIC to favour overly complex models, the model selection between the model without any adjustment terms and with one cosine adjustment term was made based on QAIC selection following the approach of Howe et al. (2019).

Image processing for one day yielded sufficient observations for data analysis for *Kobus megaceros*. For *Orxy dammah*, *Equus grevyi*, *Giraffa camelopardalis* and *Numida meleagris*, we included the second day and for *Eudorcas thomsonii* the third day to obtain an adequate sample size.

3 | RESULTS

We collected a total of 79,800 pictures. For the analysis, we processed 285 pictures for *Kobus megaceros* yielding a total of 694 observation distances, 307 pictures for *Equus grevyi* (448 observations), 300 pictures for *Giraffa Camelopardalis* (383 observations), 149 pictures for *Numida meleagris* (236 observations), 274 pictures for *Oryx dammah* (370 observations) and 285 pictures for *Eudorcas thomsonii* (393 observations) (Figure S2 Supplemental material for histograms of observed distances per species).

3.1 | Calculating animal observation distances

The estimated mean focal length of our camera model was 27.03 (SD = 0.42). Substituting this value in Equation 2, we were able to calculate observation distances that were very similar to the reference distances (Figure 1). On average, distances obtained with the photogrammetry approach were 0.28 m (SD = 0.46 m) greater than reference distances ($n = 369$). A Spearman's rank correlation test revealed a highly significant correlation ($\rho = 0.99$, $p < 0.001$) although a paired t test showed that the difference in means is small but significant ($t = 11.49$; $p < 0.05$). Only for Rothschild's giraffe, where we used knee height derived from size data on most pictures to calculate distances, and helmeted guineafowl, the difference in means was not significant (Rothschild's giraffe: MD = −0.05 m, $t = 1.04$, $p = 0.85$; helmeted guineafowl: MD = 0.06 m, $t = 0.96$, $p = 0.17$). For the remaining four species, distances derived via photogrammetry were significantly but only slightly higher than reference distances with the MD ranging from 0.33 m for Nile lechwe and Grevy's zebra to 0.38 m for scimitar oryx (Figure S4 Supporting material for results for each species).

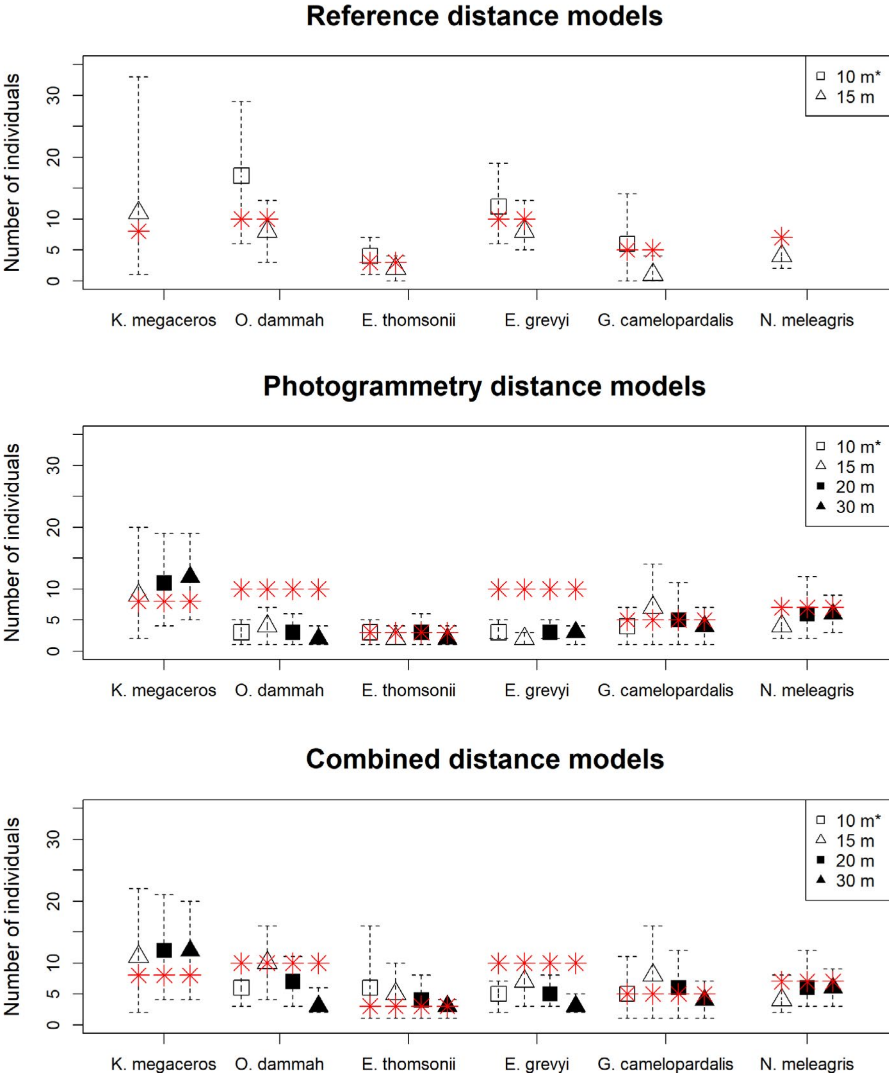

FIGURE 2 Camera Trap Distance Sampling models. Estimates and corresponding 95% confidence intervals for number of individuals per species for all CTDS models. All models were performed with a uniform key function and different truncation distances. Model selection followed QAIC (Table S2 Supplemental material for results of each model). Red stars represent actual number of individuals within the enclosure. 95% confidence intervals were obtained from non-parametric bootstrapping with 999 iterations

3.2 | Estimating population size

Estimating availability following the approach of Rowcliffe et al. (2014) with two different bandwidth multiplier values (0.8 and 1) and the manual approach of Cappelle et al. (2019) yielded very similar activity level estimates, although estimates following Rowcliffe et al. (2014) seemed to be sensitive to bandwidth selection (Table 1 and Figure S3 Supplemental material). For consistency, we therefore chose to proceed analysis with the manually estimated availabilities for each species. We do not expect this decision to influence the results of our analysis considerably and definitely do not expect any impact on the conclusions of our study. The activity levels for each species indicated that none of them were available for detection 100% of the time. Availabilities ranged from 0.56 (*Numida meleagris*) to 0.82 (*Orxy dammah*) (Table 1). Furthermore, during availability analysis, we found that there were no observations of helmeted guineafowl after 4:00 p.m., contradicting our assumption of all animals being in the enclosure until 6:00 p.m. We therefore adjusted their sampling effort accordingly.

For all three sets of models (distances derived with the reference and photogrammetry approach and the combined distance data), the abundance estimates were very similar to actual numbers of individuals within the enclosure (Figure 2 and Table S2 Supplemental material). The models performed on distances derived from reference imagery included the least observations ranging from 47 for Rothschild's giraffe to 168 for scimitar oryx. Still, actual abundance, when right truncating at the largest distance obtained (15 metres for Nile lechwe and helmeted guineafowl, 10 metres for scimitar oryx, Thomson's gazelle and Grevy's zebra and 6 metres for Rothschild's giraffe), was always within the 95% confidence interval of the model. Right truncating at 15 metres only slightly improved the accuracy of the abundance estimates compared with the real abundance for scimitar oryx.

The models conducted on the distance data obtained from the photogrammetry approach underestimated abundance for scimitar oryx and Grevy's zebra regardless of the truncation distance. For the remaining four species, the choice of truncation distance did not considerably influence the abundance estimates. All models including the ones with truncation distances of up to 30 metres produced estimates very close to actual abundances within the enclosure. Using a combined distance measure including all observations of a species slightly improved the model fit for scimitar oryx and Grevy's zebra, although with larger truncation distances, the abundance was increasingly underestimated. For the remaining species, the right truncation distance again seemed to have no significant effect on the abundance estimates.

4 | DISCUSSION

In this study, we modified and refined the CTDS methodology for the estimation of densities by applying an alternative protocol (time-lapse mode) and introducing a novel approach to deriving animal observation distances by applying photogrammetric methods. Distances derived using the photogrammetry approach were compared with distances obtained via the previously suggested method of comparing animal positions to distance labelled reference imagery.

4.1 | Deriving animal observation distances

The photogrammetry approach provided observation distances very similar to the ones obtained by assigning animals to distances by comparing their locations to reference imagery as originally proposed by Howe et al. (2017). Distances from the photogrammetry approach were on average only 0.28 metres higher than reference distances. One potential reason might be the higher resolution of the photogrammetry distances as they were calculated with a precision of two decimal places while reference distances were assigned to the nearest 50 cm interval. In addition, with increasing distance, we expect small measuring errors to have an increasing effect on the distances estimated using photogrammetry. But since assigning distances with reference imagery also becomes more challenging with increasing distances as differences of one or two metres become less apparent, it is already recommended to group distances into intervals of up to 5 metres for CTDS analysis anyway. We therefore do not expect slightly inaccurate assignments of observation distances, or the higher resolution obtained in our study, to be a major source of error in camera trap distance sampling. Still, as we only used animal size information from literature, our results could potentially be improved by the possibility to estimate shoulder height of animals more precisely. For field studies, we therefore recommend the installation of a scale rod for height measurement of animals. If a measuring rod is placed in front of the camera, shoulder height could be more precisely measured whenever an animal moves past it.

We also recognise that this approach of deriving animal observation distances comes with certain limitations for field studies. It will only be functional, if intraspecific size variation (e.g. sexual dimorphism) is absent or small or if males and female are clearly distinguishable. In addition, our study did not include any juvenile animals making it easier to calculate distances, an issue that must be addressed in studies with a more diverse demographic structure. Also, we found it difficult to calculate distances to animals directly in front of the camera (up to 3 metres depending on size of the animal) or where the animal was only partly visible. This limitation should be avoided by grouping those distances into one distance interval (e.g. 0 to 3 metres) or if enough data are available left truncate data at 3 metres.

Yet, regardless of the above-mentioned limitations, we find that the photogrammetry approach is a promising technique to derive accurate observation distances especially in open habitats such as steppes, savannahs or meadows with little vegetation obscuring the field of view. One of its most powerful advantages is that if the focal length of the specific camera type is obtainable, it might even enable the application to previously collected data, opening the possibility to apply CTDS retrospectively to a huge amount of already existing data sets. As more advanced digital methods to estimate observation distances, such as by computer vision techniques, are already in development, an automated process of distance calculation based on photogrammetric methods further reducing the effort currently involved with assigning observation distances might also be conceivable.

4.2 | Comparing estimated and true animal abundance

We have shown that CTDS generated mostly accurate estimates of population sizes compared with actual numbers within the enclosure regardless of the distance data used and the truncation distance. Only for *Equus grevyi* and *Oryx dammah*, abundance was almost always underestimated, especially with the model using distances obtained via photogrammetry. This problem might be related to the distribution of observed distances, due to the necessity to attach most cameras at the edge of the enclosure and the lack of observations below 3 metres in the photogrammetry distance data. A potential solution is to left truncate the data at 3 metres, which was not done in our analysis to keep consistency between the photogrammetry and the combined distance data models. Also, for the remaining four species, this lack of data seemed to be compensated by adding an adjustment term to the uniform key function. However, as distance sampling assumes a random placement of the cameras with regard to animal movement, this assumption is most likely violated by our CT placement. Poor results regarding *Equus grevyi* and *Orxy dammah* might therefore also be associated with the movement of the animals (e.g. avoidance of or attraction to edge areas) and the resulting distribution of observation distances rather than sampling problems with CTDS. For example, for *Orxy dammah* in the combined distance model, we have a disproportionately high number of observations between 0 and 3 metres from the camera indicating a preference of areas close to the fence or even an attraction to the cameras and potentially impairing model fit especially with large truncation distances.

As CTDS uses the same framework and software as standard distance sampling, there are numerous possibilities of further extending it to also include additional covariates, for example environmental variables (Marques & Buckland, 2003; Oedekoven et al., 2013; Royle et al., 2004) in the analysis or to embed it into density surface modelling (Miller et al., 2013). We highly recommend more studies considering further extensions to CTDS and also evaluating, for example the use of paired cameras for distance estimation, the automation of species recognition or experimenting with different time intervals *t* between snapshot moments to increase the independence of observations. We acknowledge that CTDS surveys of free-ranging animals certainly require a much larger survey effort than used in our study, given the unusual good availability and high density of animals within the enclosure.

4.3 | Potential for application with other taxa

The use of time-lapse CT settings opens various new possibilities for future CT surveys applying CTDS to estimate density or abundance. Our study shows that abundances obtained from the photogrammetry approach data set were still very accurate compared with true abundances even with truncation distances of up to 30 metres, a distance that could not be achieved by using PIR sensors only. Moreover, it could make the CTDS methodology more easily applicable also to poikilothermic species or species with small body sizes that do not trigger remote camera devices. CTDS might even be usable in insect studies (e.g. *Lepidoptera* or *Hymenoptera*) if camera resolution is high enough to obtain clear pictures on which species can be identified. Already existing studies applying distance sampling methodology to, for example butterfly counts (Hamm, 2013; Isaac et al., 2011) report that ad hoc species identification combined with distance assignment have proven to be difficult due to the intense effort of butterfly surveys (Isaac et al., 2011). If species can be distinguished phenotypically, CTs could improve both, as species and distance data can be derived from pictures or videos during the analysis. If size data for the species of interest are available, the photogrammetric method of measuring distances presented in this paper might even be possible to use for butterflies and other large arthropods. Further implementations and evaluation of CTDS would be needed to support this idea.

5 | CONCLUSION

With our study, we were able to further validate the reliability and accuracy of CTDS. We extended the previously proposed protocol by using the time-lapse mode instead of the triggering mode and by using a photogrammetry approach to derive animal observation distances. With the use of time-lapse mode, any camera that can be programmed to record pictures or videos at predefined time intervals may be used. This offers new possibilities for further applications on a broad range of taxa, especially those unable to trigger remote camera systems. Using photogrammetry to obtain observation distances presents a novel approach that is potentially able to even be applied to already existing data sets. More automated techniques following this methodology might further decrease the amount of work currently associated with extracting observation distances.

We highly recommend a field test of the photogrammetric methodology and the application of CTDS in future animal surveys and see great potential in developing further extensions and modifications to this method.

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CONFLICT OF INTEREST

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

AUTHOR CONTRIBUTIONS

A.Z. and H.K. developed the idea of the project and carried out the fieldwork in the zoological garden. A.Z. performed the analysis of the pictures and the statistical analysis and wrote the manuscript. H.K. provided assistance with the statistical analysis and revised the manuscript during the process. R.H. provided the necessary input from the zoological garden, contributed to the final version of the manuscript and gave the final approval for submission. H.K. supervised the project.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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