

Estimating animal abundance and effort–precision relationship with camera trap distance sampling

NOÉMIE CAPPELLE ^{1,†} ERIC J. HOWE ² CHRISTOPHE BOESCH,¹ AND HJALMAR S. KÜHL^{1,3}

¹Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

²Centre for Research into Ecological and Environmental Modeling, the Observatory, University of St Andrews, Fife, UK

³German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Citation: Cappelle, N., E. J. Howe, C. Boesch, and H. S. Kühl. 2021. Estimating animal abundance and effort–precision relationship with camera trap distance sampling. *Ecosphere* 12(1):e03299. 10.1002/ecs2.3299

Abstract. Effective monitoring methods are needed for assessing the state of biodiversity and detecting population trends. The popularity of camera trapping in wildlife surveys continues to increase as they are able to detect species in remote and difficult-to-access areas. As a result, several statistical estimators of the abundance of unmarked animal populations have been developed, but none have been widely tested. Even where the potential for accurate estimation has been demonstrated, whether these methods estimators can yield estimates of sufficient precision to detect trends and inform conservation action remains questionable. Here, we assess the effort–precision relationship of camera trap distance sampling (CTDS) in order to help researchers design efficient surveys. A total of 200 cameras were deployed for 10 months across 200 km² in the Taï National Park, Côte d’Ivoire. We estimated abundance of Maxwell’s duikers, western chimpanzees, leopards, and forest elephants that are challenging to enumerate due to rarity or semi-arboreality. To test the effects of spatial and temporal survey effort on the precision of CTDS estimates, we calculated coefficient of variation (CV) of the encounter rate from subsets of our complete data sets. Estimated abundance of leopard and Maxwell’s duiker density (20% < CV < 30% and CV = 11%, respectively) were similar to prior estimates from the same area. Abundances of chimpanzees (20% < CV < 30%) were underestimated, but the quality of inference was similar to that reported after labor-intensive line transect surveys to nests. Estimates for the rare forest elephants were potentially unreliable since they were too imprecise (60% < CV < 200%). Generalized linear models coefficients indicated that for relatively common, ground-dwelling species, CVs between 10% and 20% are achievable from a variety of survey designs, including long-term (6+ months) surveys at few locations (50), or short term (2-week to 2-month) surveys at 100–150 locations. We conclude that CTDS can efficiently provide estimates of abundance of multiple species of sufficient quality and precision to inform conservation decisions. However, estimates for the rarest species will be imprecise even from ambitious surveys and may be biased for species that exhibit strong reactions to cameras.

Key words: chimpanzee; design; elephant; leopard; Maxwell’s duiker; monitoring; precision; sampling effort.

Received 25 July 2019; accepted 10 August 2020; final version received 7 October 2020. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** noemie_cappelle@eva.mpg.de

INTRODUCTION

Camera traps (CT) that detect wildlife using heat or motion sensors can detect a wide variety

of wildlife including rare, nocturnal, and elusive species. They are particularly useful for monitoring biodiversity over large areas, and in habitats with poor visibility and limited access (Rovero

et al. 2010, Burton et al. 2015, Rovero and Zimmermann 2016). As a consequence, CTs are now used worldwide in monitoring programs. However, well-developed approaches to estimating animal population size, such as capture–recapture or spatially explicit capture–recapture (Karanth 1995, Després-Einspenner et al. 2017), are limited to animals that are individually identifiable. Rowcliffe et al.’s (2008) random encounter model (REM) was the first estimator of absolute abundance from CT data that did not rely on marked or recognizable individuals. Many other estimators have been proposed, but most have had little evaluation or testing (Chandler and Royle 2013, Howe et al. 2017, Campos-Candela et al. 2018, Moeller et al. 2018, Nakashima et al. 2018, Gilbert et al. 2020, Luo et al. 2020). Chandler and Royle’s (2013) spatial count models require intensive sampling and yield imprecise estimates. All other estimators require randomized sampling and include both spatial and temporal components to account for the small area within which detection by CTs can be assumed to be high or certain, and animal movement. The REM, the model proposed by Campos-Candela et al. (2018), and the random encounter staying time (REST) model (Nakashima et al. 2018) are all based on ideal gas models predicting collision rates; an estimator for animal density can be derived from the rates of contact between animals and camera traps (Hutchinson and Waser 2007, Rowcliffe et al. 2008). The REM and Luo et al.’s (2020) methods require accurate estimates of day range or the speed of animal movement, which may be difficult to obtain or to estimate precisely. The REST is an extension of the REM that substitutes staying time (i.e., the amount of time detected animals remains within a specific area within the field of view of a camera trap) for the speed of movement. Campos-Candela et al.’s (2018) model replaces speed movement with home range size based on the principle of association, defined as the number of ongoing occurrences within a given area and at a given instant (Hutchinson and Waser 2007).

Camera trap distance sampling (CTDS) extends point transect distance sampling methods to account for the fact that CTs monitor a sector within which detection is imperfect and a function of distance from the camera. Rather than relying on estimates of home range size,

animal speed, day range, or staying time, CTDS accounts for animal movement by recording observation distances at predefined snapshot moments. It relies on the usual assumptions of distance sampling surveys of live animals: (1) lines or points are placed independently of the distribution of animals, (2) animals on the line or point are detected with certainty, (3) animals are detected at their initial location prior to any movement in response to the observer, and distance measurements are accurate (Buckland et al. 2001). Observations of distance from CTDS surveys are not independent, because multiple observations of distance to the same animal(s) are recorded during a single pass by an animal or group of animals in front of a CT (to avoid potential positive bias in observed distances; Howe et al. 2017). Independence of observations is not a critical assumption of DS methods: violations are not expected to affect point estimates of abundance, but they render P values of goodness-of-fit tests and model selection criteria invalid, and variance may be underestimated with analytic estimators; bootstrapping generally improves confidence interval coverage in these situations (Buckland et al. 2001, Fewster et al. 2009, Howe et al. 2017). Temporally limited availability for detection must be accounted for to avoid negative bias in CTDS estimates, but the proportion of time active is estimable from the CT data (Rowcliffe et al. 2014, Cappelle et al. 2019). See Howe et al. (2017) for a more detailed description of CTDS including assumptions and practical considerations, and Gilbert et al. (2020) for a recent review and comparison of abundance estimators with camera traps.

All of the models mentioned above have had their accuracy tested using simulations, and in some cases with field data, but none has been demonstrated to consistently yield accurate estimates for a variety of species under field conditions. There has been ongoing development of the REM framework (Rowcliffe et al. 2011, 2014, 2016, Lucas et al. 2015, Gilbert et al. 2020, Jourdain et al. 2020), but practical applications have had mixed success due to inappropriate survey design or difficulties estimating the speed of animal movement (Rovero and Marshall 2009, Zero et al. 2013, Anile et al. 2014, Cusack et al. 2015, Balestrieri 2016, Caravaggi et al. 2016). Nakashima et al. (2020) estimated densities and

relationships between density and habitat covariates for sympatric duiker species and concluded that the method could be effective for estimating ungulate densities. Cappelle et al. (2019) applied CTDS, line transect distance sampling of nests, and spatially explicit capture–recapture to a habituated chimpanzee community of known size. The CTDS estimate of abundance was accurate (relative bias was only 0.2%), but imprecise (coefficient of variation [CV] \approx 40% of the estimate). Trends can be detected only with accurate and precise estimates (Nichols and Williams 2006, Si et al. 2014), and Howe et al. (2017) and Cappelle et al. (2019) recommended maximizing the number of sampling locations (rather than survey duration) to improve precision, but no data were presented regarding the performance of CTDS at varying spatial and temporal sampling effort. Bessone et al. (2020) used CTDS to estimate densities of 14 species from a large-scale survey in Salonga National Park, Democratic Republic of the Congo. Authors identified low detectability and reactivity to the camera as potentially important sources of bias but concluded that CTDS could allow for rapid assessments of wildlife population status and trends to inform conservation strategies.

We applied CTDS to multiple species at a large spatial scale over an extended period of time in Taï National Park (TNP), Côte d'Ivoire. In addition to information about animal abundance in one of the only remaining primary rainforests in West Africa, we were interested in quantifying relationships among survey effort (spatial and temporal), animal density, and the precision of CTDS estimates of abundance, including for species that are particularly challenging to enumerate due to rarity or semi-arboreal behavior. Ideally, we would have subsampled complete data sets from multiple species hundreds or thousands of times and analyzed each subsample to estimate density its variance. However, model fitting, model selection, and especially variance estimation by bootstrapping (further subsampling and reanalyzing each subset 500–1000 times) would have become prohibitively time-consuming. Fortunately, because animals are often patchily distributed and move non-randomly, whereas sampling locations are randomly selected, the encounter rate component of the variance usually dominates the

overall variance in animal densities estimated from DS surveys, including CTDS surveys (Buckland et al. 2001, Fewster et al. 2009, Howe et al. 2017). We therefore estimated the encounter rate component of the variance from hundreds of randomized spatiotemporal subsets of the complete data sets from species occurring at different densities to quantify the relationships between spatial and temporal sampling effort and the precision of estimates of the encounter rate, as a proxy for the relationships between effort and the precision of density estimates. We expect our results to help researchers select among available methods for enumerating wildlife, and to design efficient multispecies CTDS surveys that yield estimates of sufficient precision to inform management and conservation activities.

MATERIALS AND METHODS

Study site and chimpanzee's true population size

The field survey took place in Taï National Park (TNP), Côte d'Ivoire (5°08' N to 6°40' N, and 6°47' W to 7°25' W; Fig. 1). This park is one of the largest remaining tracts of undisturbed lowland rainforest in West Africa, spreading over 5400 km². The average annual rainfall in the area is approximately 1800 mm and the annual average temperature is between 24°C and 30°C (Anderson et al. 2005).

The study area was in the western area of the park, where six stable social groups of chimpanzees occur (Fig. 1). Four of them (the North, Middle, South, and East groups) have been habituated to humans over several years by Taï Chimpanzee Project researchers and field assistants (Boesch et al. 2006, 2008). These groups are followed on a daily basis; all individuals have names and their ages are known (individuals, North $n = 20$; Middle range estimated between 1 and 3; South $n = 36$, and East $n = 32$). At the time of the study, another group was undergoing habituation (North-East) with the group size approximately known (range estimated between 35 and 60 individuals). The size of an unstudied group (West group; Boesch et al. 2008) was also approximately known from observations of inter-group encounters (range estimated between 7 and 10 individuals; S. Lemoine, *personal communication*).

Camera traps were deployed throughout the smaller territories of the West and Middle

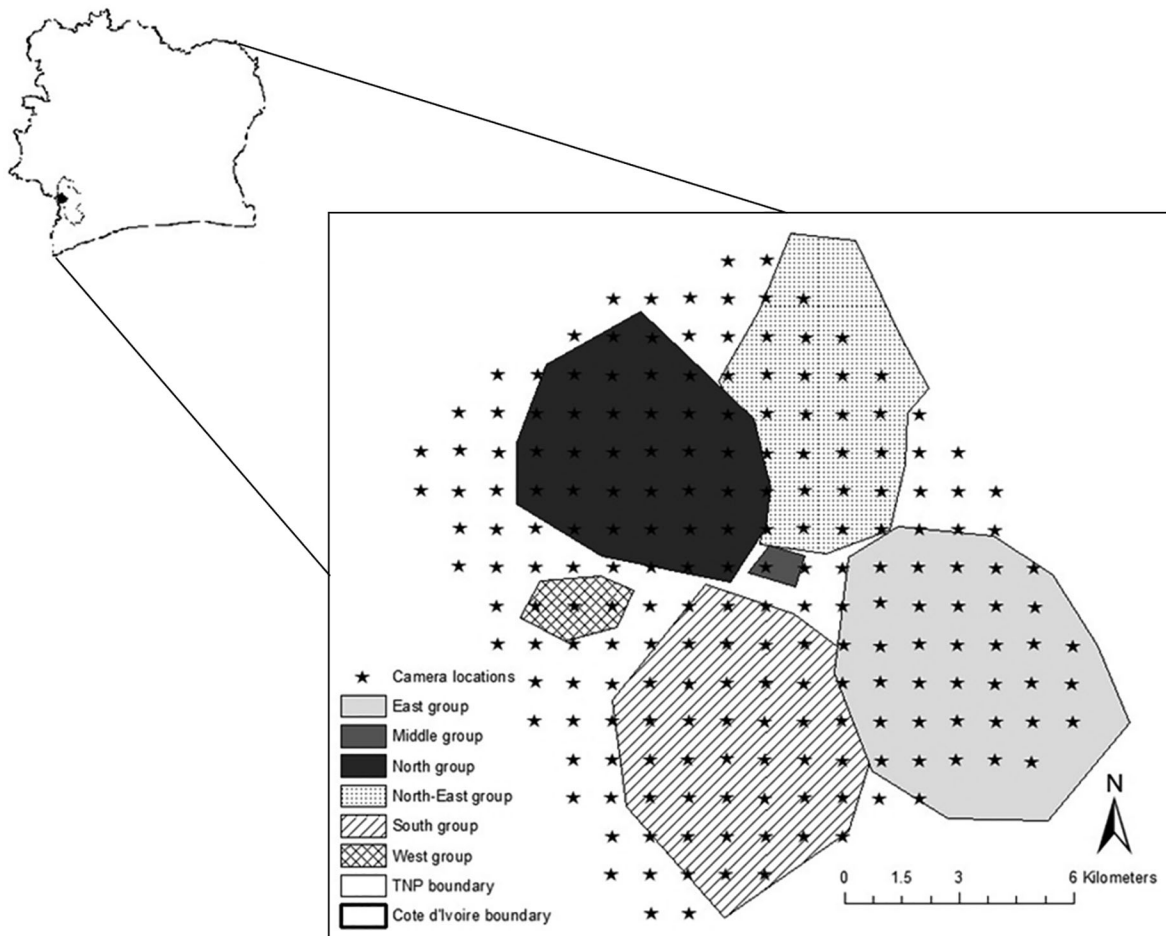


Fig. 1. Location of cameras and the study area in the Tai National Park (TNP).

groups, and over most of the larger territories of the East, North-East, North, and South groups. Thus, the exact true population size within the surveyed area during sampling is unknown, but we are confident that between 131 and 161 chimpanzees were living in and around it.

Field data collection

We deployed 200 CTs in a systematic grid with 1-km spacing and a random origin within our 200-km² study area (Fig. 1) in October 2016. All CTs were installed by mid-December and removed in August 2017. Camera traps (Bushnell Trophy Cam; <http://bushnell.com>) were installed within 30 m of the design-specified locations, at a height of 0.5 m, oriented approximately north ($\pm 20^\circ$). Two cameras did not function and one was destroyed by a poacher, so data were

collected at only 197 locations. We programmed the cameras to record 10–60 s videos when triggered (not all cameras could be programmed to record 60 s videos), and set the motion sensor to high sensitivity. At each location, reference videos of researchers holding signs indicating distances from the camera (from 1 to 15 m at 1-m intervals, in the center, and at each side of the camera's field of view) were recorded so that we could subsequently measure distances to filmed animals (see Howe et al. 2017 for details).

Video processing

We initially processed all videos to record the species and number of individuals detected, along with the location, date, and time of recording. Where species identification was not possible, we recorded the genus. We then selected

four medium- to large-bodied species that occur at very different densities, three of which are expected to be particularly difficult to enumerate using CTDS due to their rarity or semi-arboreal behavior: (1) forest elephants (*Loxodonta africana cyclotis*; very rare), (2) leopards (*Panthera pardus*; rare, semi-arboreal), (3) western chimpanzees (*Pan troglodytes verus*; uncommon, semi-arboreal), and (4) Maxwell's duikers (*Philantomba maxwelli*; common; Jenny 1996, Tiedoué et al. 2016, WCF 2016, Howe et al. 2017). We measured distances between CTs and the midpoints of individuals of these species at predetermined snapshot moments two seconds apart (at 0, 2, 4, . . . , 58 s after the even minute) for as long as they were visible, by comparing videos of animals to reference videos showing distance markers. Animals were assigned to 1-m distance intervals from 0 to 8 m. As larger distances were more difficult to measure precisely observations >8 m were assigned to one of the following categories: 8–10 m, 10–12 m, 12–15 m, and beyond 15 m.

The duration of the time interval between snapshot moments (t) is at the discretion of researchers, and selected to minimize missed detections of rare or fast-moving animals without accumulating unmanageable numbers of observations of common or slow-moving animals (because measuring distances is time-consuming, and uncertainty in detectability usually contributes only a small fraction to the overall variance of density estimates; Howe et al. 2017:1559). Howe et al. (2017) suggested 0.25–3.00 s; optimal species-specific values have not been identified. We chose a two-second interval because a shorter interval was not necessary to avoid missed detections of the species sampled, and for the sake of consistency with prior studies (Howe et al. 2017, Cappelle et al. 2019, Bessone et al. 2020).

Data analyses

Availability for detection and temporal sampling effort.—The CTDS method overestimates survey duration (T_k of Eq. 1 below) and therefore underestimates abundance unless the proportion of time when animals are not available for detection is accounted for. This proportion of time can be estimated either by defining T_k as only a subset of the hours within each day, and/or correcting for limited availability within T_k (Howe et al.

2017). Data were insufficient to calculate the availability of elephants, so we considered that they were available for the camera between the start time of the first video to the end of the end time of the last video (5:00–17:59). T_k was defined as 12 h 59 min and 59 s (or 46,799 s) \times the number of camera-days for the elephants.

We obtained abundant data from Maxwell's duikers—so much that measuring distances to all of them would have been very time-consuming and unnecessary. We therefore only included data from duikers filmed during the two peaks of activity (7:00–7:59, and 17:00–17:59) and defined survey duration for duikers as 1 h and 58 min (or 7198 s) \times the number of camera-days. Leopards and chimpanzees were likely not available for detection at all times included in T_k for these species, that is, during periods of inactivity and time spent outside the vertical range of CTs (in trees). Sufficient data were collected to estimate daily availability of the leopards and chimpanzees. We therefore defined T_k for semi-arboreal species as 24 h and estimated the proportion of each 24-h day that these species were available for detection using methods described in Rowcliffe et al. (2014; ARo), and Cappelle et al. (2019; ACa). Both methods require the assumption that 100% of the population was available for detection during the daily peak of activity. For Maxwell's duikers, we did not adjust for limited availability during daily peaks of activity, but assumed 100% of the population was available at these times.

To avoid overestimating temporal sampling effort on days when animals may have been displaced away from cameras by researchers visiting them (e.g., to replace batteries or memory cards), or when cameras were not functioning, we excluded all data from those days.

Abundance estimation.—We estimated densities using Distance 7.1 (Thomas et al. 2010) using the following equation for camera trap point transects:

$$\hat{D} = \frac{\sum_{k=1}^K n_k}{\pi w^2 \sum_{k=1}^K e_k \hat{P}_k} \times \frac{1}{\text{activity level}} \quad (1)$$

where $e_k = \theta T_k / 2\pi t$ is the sampling effort at point k , T_k is the temporal sampling effort at point k in seconds, t is the length of the time step between snapshot moments (2 s), θ is the central angle of

field of view of the camera in radians, w is the truncation distance beyond which any recorded distances are discarded, n_k is the number of observations of distance to animals at point k , and \hat{P}_k is the probability that an individual is detected by the sensor and an image obtained when within the field of view of the camera at a snapshot moment, estimated by modeling the distance data (Howe et al. 2017). We estimated population sizes by multiplying density estimates by the study area size (200 km²; Fig. 1).

Attraction to or avoidance of CTs (observers) violates one or more standard assumptions of distance sampling and can cause bias (Buckland et al. 2001, Marshall et al. 2008, Marini et al. 2009, Howe et al. 2017, Bessone et al. 2020). To minimize this bias, we first excluded all videos where individuals were showing obvious signs of interest in the CT and remained in front of it for more than 60 s. We then investigated deviations from expected numbers of observations within different distance categories using the χ^2 goodness-of-fit (GOF) test for binned distance data (Buckland et al. 2001:71, Eq. 3.57) and inspected plots of fitted probability density functions of observed distances and of the estimated probability of detection as a function of distance against scaled histograms of distance observations to determine left-truncation points that resulted in the best fit. Both leopards and chimpanzees often showed strong attraction to cameras (though some chimpanzees exhibited avoidance), and more observations than expected were recorded between 0 and 2 m, so we left-truncated these data sets at 2 m. There was no attraction or avoidance of the cameras apparent in videos of Maxwell's duikers, and only slightly fewer than expected observations close to the camera, so we did not censor or left-truncate those data. We right-truncated distance observations >15 m for leopards, chimpanzees, and Maxwell's duikers, because longer distances were difficult to measure accurately. Data from elephants were sparse and most models of the detection function did not fit well. We achieved a reasonable fit only when we did not left-truncate and right-truncated at 8 m, while combining distance observations into 2 m intervals.

Frequently, Akaike's information criterion (AIC) is used to select among multiple candidate models of the detection function, including

models with adjustment terms, which can improve fit (Buckland et al. 2001). However, the overdispersion introduced by non-independent detections causes AIC to select overly complex models of the detection function (Buckland et al. 2001, 2010, Burnham and Anderson 2002). Furthermore, models with adjustment terms were frequently not monotonically non-increasing when fit to our data. We therefore considered only simple, unadjusted half-normal and hazard rate models of the detection function to avoid overfitting (Buckland et al. 2004, 2010, Marques et al. 2007), and inspected fitted probability density functions of observed distances and plots of the estimated probability of detection as a function of distance against scaled histograms of distance observations to select between models, and to verify that fits were monotonically non-increasing. We estimated variances two ways: (1) using the default analytic variance estimators in Distance 7.1, which use $\widehat{\text{var}}_{p2}$ of Fewster et al. (2009: Eq. 24, Web Appendix B) for the encounter rate component of the variance, and from 999 non-parametric bootstrap resamples (with replacement) of data from different points (Buckland et al. 2001, Howe et al. 2017). For each species and variance estimator, we calculated the CV of the density estimate as the point estimate divided by the square root of the variance.

Spatiotemporal sampling effort and precision.—We quantified the effects of spatial and temporal survey effort on the precision of CTDS abundance estimates by subsampling our complete data sets, calculating the encounter rate and its variance for each subsample, and fitting regression models with the species-specific CV of the encounter rate as the response variable, and the number of sampling locations and the mean number of sampling days per location as predictors. The complete data set comprised 30,195 camera-days from 197 locations on 314 consecutive days. We first defined fixed spatial subsets of data from the first 55 and 102 cameras deployed and fixed temporal subsets of the data from the start of sampling to the end of 2016, and from the start of sampling through March of 2017. Fixed spatial and temporal subsets comprised approximately one half and one quarter of the total sampling locations and durations, respectively (Table 1). Subsets of locations were contiguous in space and located where CTs were deployed

Table 1. Total numbers of locations where and day when sampling occurred, mean numbers of effective sampling days per location, and total camera-days of sampling in different fixed spatial and temporal subsets of our complete survey.

Data set	No. locations	No. days	Mean no. sampling days/location	No. camera-days	Subsample sizes†
Complete	197	314	153.3	30,195	2, 5, 10, 15, 20, 25
Half locations	102	306	147.0	14,990	2, 5, 10
Quarter locations	55	291	130.6	7181	2, 5
Half duration	193	165	91.8	17,722	2, 5, 10, 15
Quarter duration	190	75	37.3	7078	2, 5

Notes: Locations exclude those where cameras never functioned, and mean sampling days per location and camera-days include only days when cameras functioned and were not visited by researchers. Also shown are numbers of camera-days subsampled from each subset (100 random samples of each size were selected from each respective data set; see *Materials and Methods*).

† Sizes of subsamples of camera-days (thousands).

earliest, and temporal subsets were continuous in time and included the beginning of the survey. Thus, our fixed spatial and temporal subsets mimicked real surveys over smaller areas, and shorter durations, respectively. We then selected one hundred random subsamples, without replacement, of 2000, and multiples of 5000, camera-days, up to a maximum of 25,000 camera-days, from the complete data set and each fixed subset thereof (Table 1). Subsampling yielded a total of 1700 data sets representing 17 different design scenarios (Table 1).

The empirical, design-based variance of densities estimated by CTDS includes components for both detection probability and encounter rate (Fewster et al. 2009). The encounter rate variance is often the dominant contributor to the overall variance in density (Fewster et al. 2009, Howe et al. 2017). Therefore, to simplify the analyses of the many subsets of the data, we did not estimate density, and we ignored the detection probability component of the variance. Rather, for each subsample of camera-days, we calculated the encounter rate as the total number of observations of animals (n) divided by the total effort (as the sum of e_k of Eq. 1 across all days and locations included in the subsample; Fewster et al. 2009:230), and the variance of the encounter rate as $\widehat{\text{var}}_{p2}$ of Fewster et al. (2009). Coefficient of variations of encounter rates were calculated as the square root of the $\widehat{\text{var}}_{p2}$ divided by the point estimate.

We initially fit linear regression models with the CV of the encounter rate as the response variable, and the number of sampling locations and the mean duration of sampling (in days) per

location as predictors. Diagnostic plots revealed skewness in the raw data and the residuals, and evidence of heteroscedasticity, so we fit generalized Linear Models (GLM; McCullagh and Nelder 1989) with a gamma error structure and inverse link function to the same data. There was no evidence of overdispersion after fitting the GLMs (range of dispersion parameters = 1.001–1.002). We used the estimated GLM coefficients to predict CVs of the encounter rate from a range of theoretical surveys for species occurring at different densities. We also predicted CVs of encounter rates from GLM coefficients and information describing survey effort in previously published CTDS surveys (Howe et al. 2017, Cappelle et al. 2019, Bessone et al. 2020), and compared our predictions to reported CVs of density.

RESULTS

Data collection and video processing

It took one crew of two people approximately one day to install CTs and record reference videos at four locations. A total of two months was required to set up cameras in 200 locations. Cameras were left in place for a total of 59,380 camera-days (equivalent of about 297 d per camera), but camera theft, memory card capacity, and battery life reduced the total camera trap effort to 33,237 camera-days (168 d/camera). After removing data from days when cameras were being installed or visited by researchers, a total of 30,195 camera-days remained (153 d/camera).

We obtained 82,806 videos of which 36,937 (almost 45%) included no animals, because CTs

were either triggered by moving foliage or animals moving so quickly that they left the field of view within the trigger speed of the CT, or malfunctioned, recording videos every minute until the batteries were drained. In the end, 45,869 videos included animals. We were able to identify over 90% of the filmed animals to species and recorded 77 different species.

Abundance estimation

Sample sizes varied among species, with 18 videos from only three locations yielding 503 observations of distances to elephants, to 3537 videos from 174 locations yielding 41,386 observations of distances to Maxwell's duikers (Table 2).

We estimated that chimpanzees were available for detection 36% of the time each day using ARo (Fig. 2) and 73% during daytime interval, but ACa yielded an estimate of 27% over the same time interval and 49% between daytime interval. Independent data from direct observations of the well-habituated groups (Doran 1989), showed that males were active on the ground for a larger proportion of each day than females, but females made up more than half of the population; sex-ratio weighted average availability (ADO) was 51% over the daytime interval. Availability of leopards estimated using ARo was 55% of the time each day and 40% using ACa.

The unadjusted hazard rate model and the unadjusted half-normal model of the detection function were the only valid models for elephants and leopards, respectively. The hazard rate model provided a better fit to our duiker data (Figs. 3, 4) than the half-normal model. We were concerned that the avoidance behavior

some chimpanzees exhibited induced heterogeneity in detectability, in which cases the hazard rate key function may appear to fit well, but underestimates abundance (Buckland et al. 2004, Buckland 2006), so we estimated chimpanzee density from the half-normal model. Plots of fitted probability density functions and probabilities of detection revealed a reasonably good fit to data from duikers, but also the potential for problems in data from other species (Figs. 3, 4). More observations of leopards than expected were recorded in the first distance interval, data from chimpanzees showed fewer than expected detections within 6 m of the camera, and the probability of detecting elephants dropped sharply within the first of only four distance intervals (Figs. 3, 4).

Density estimates indicate that duikers (19.744/km²) were approximately 40 times more abundant than chimpanzees ($\approx 0.5/\text{km}^2$), and approximately 400 times more abundant than leopards and elephants ($\approx 0.05/\text{km}^2$; Table 3). We estimated that 13 elephants, 10–14 leopards (depending on availability estimator), 87–109 chimpanzees (depending on availability estimator), and 3949 Maxwell's duikers occupied our 200-km² study area (Table 3). Estimates for duikers were the most precise (CV = 11%); estimates for chimpanzees were reasonably precise (20% < CV < 30%), and estimates for elephants were potentially too imprecise to be useful (50% < CV < 200%; Table 3). The analytic estimator yielded variances that were larger than those estimated by bootstrapping (except for very rare elephants), and only slightly larger than the variance of the encounter rate calculated from the raw data (Table 3).

Table 2. Sample sizes of videos of each species (total obtained during the survey, excluded because of behavioral responses to camera traps, and considered for distance analysis), the number of locations where species were filmed, and the total number of observations of distance (n) included in analyses to estimate abundance (after excluding entire videos and truncating distance observations).

Species	No. videos			No. locations	n	No. individuals
	Total	Excluded	Considered			
Elephant	21	3	18	7	503	32
Leopard	283	96	187	60	651	147
Chimpanzee	330	15	315	87	5519	866
Maxwell	20,250	16,713	3537	174	41,202	5100

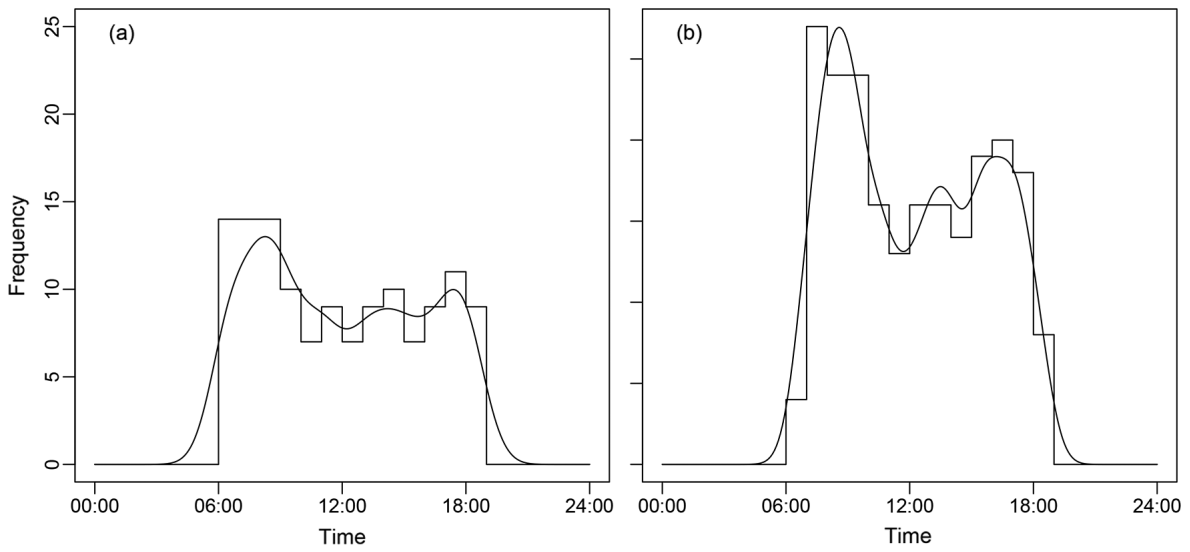


Fig. 2. Distribution of videos as function of time of day for leopards (a) and chimpanzees (b) at the study site in Tai National Park. Histograms are observed frequencies, and lines are fitted circular kernel distributions.

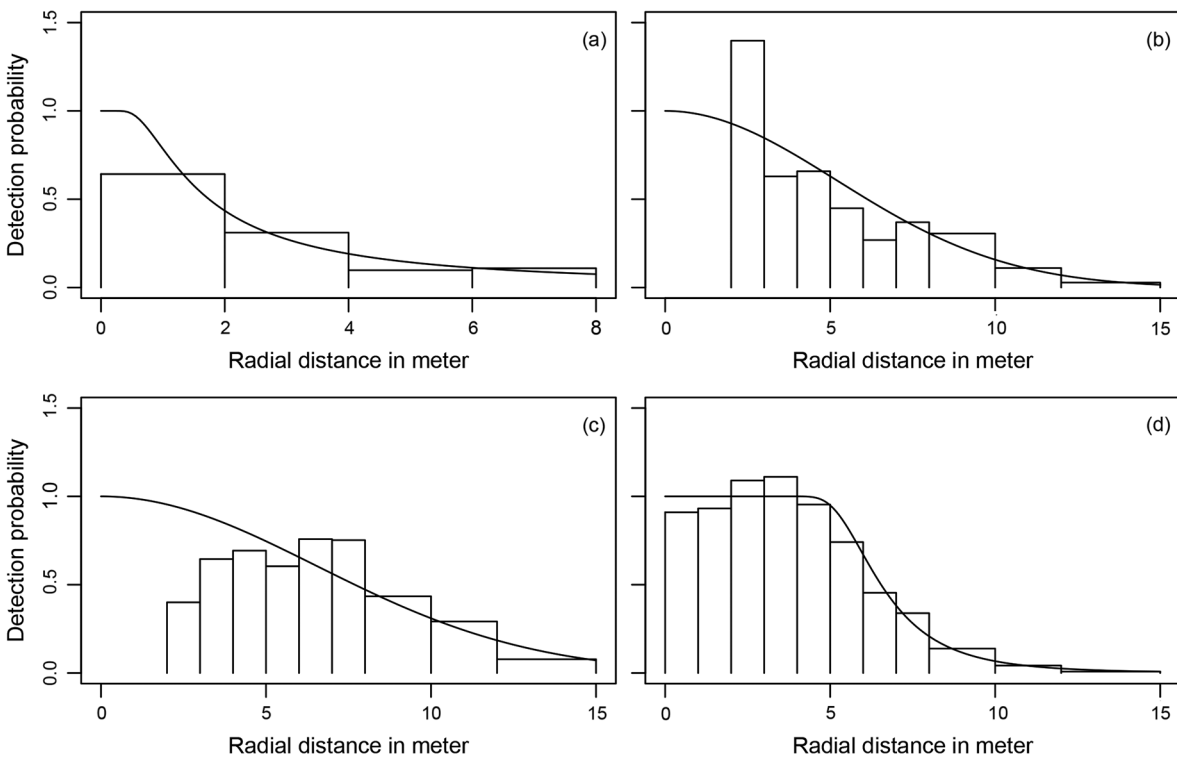


Fig. 3. Scaled histogram of the probability of detecting elephants (a), leopards (b), chimpanzees (c) and Maxwell's duikers (d), as a function of distance.

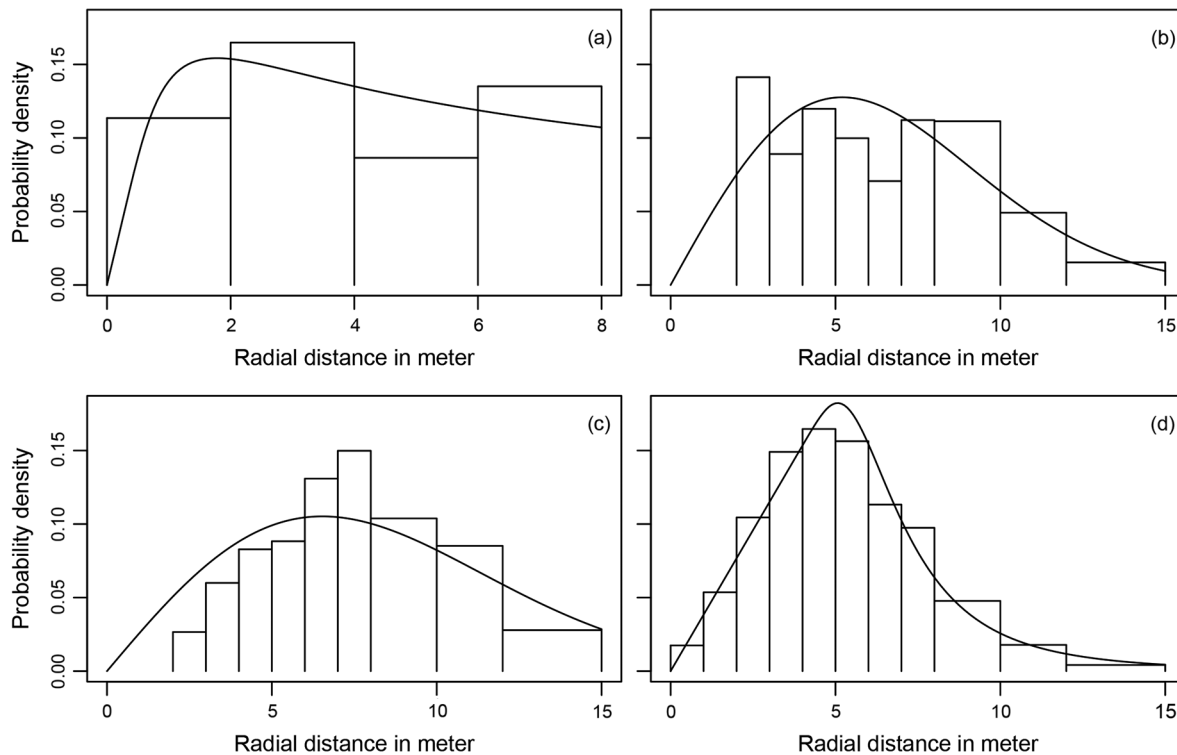


Fig. 4. Probability density functions of observed distances to elephants (a), leopards (b), chimpanzees (c) and Maxwell's duikers (d).

Spatiotemporal sampling effort and precision

Increasing the number of sampling locations had a slightly larger effect than the duration of sampling per location (in days) on the precision of estimates of duiker encounter rates, but a considerably larger effect on the precision of chimpanzee encounter rates (Table 4). Estimated coefficients for leopards (not presented) indicated only a small effect of number of locations. Additional exploratory analyses showed that (1) a large fraction of the observations of leopards came from relatively few cameras and camera-days, (2) removing approximately half of our locations dropped the few locations with the most observations, reducing average encounter rates but also providing a more even distribution of observations across locations and therefore a lower CV variance, and (3) further reducing the number of locations removed most observations of leopards, such that estimates of the encounter rate were much lower with high variances.

Our predictions suggest that for ground-dwelling species as common and detectable as duikers,

CVs will always be >20% with 25 or fewer locations, and that with 50 locations, >100 effective sampling days per location would be required to achieve a CV of 20% (Fig. 5). Increasing the number of sampling locations from 25 to 150 should yield considerable gains in precision, and having more sampling locations is increasingly important with shorter survey durations (Fig. 5). Predictions further suggest that researchers could achieve CVs as low as 20% from surveys with at least 100 sampling days at as few as 50 locations, but that for rapid (e.g., 2-week to 2-month) surveys or surveys designs that involve removing cameras to new areas this frequently, 100–140 sampling locations would be required to yield similar precision. Coefficient of variations as low as 10%, if achievable, would require >200 sampling locations even with long (>130 d) survey durations. Predicted CVs of chimpanzee encounter rates remained >30% except where survey effort approached the maximum we achieved in the field. Decreasing slopes and comparisons to Bessone et al. (2020) suggest that further

Table 3. Estimates of animal density (per km²), with lower and upper confidence limits (LCL and UCL) and percent coefficients of variation (%CVs) calculated from bootstrap and analytical (empirical design-based) variances.

Species	Species detection function†	Estimate	Density							N		
			Bootstrap variance			Empirical designed-based variance						
			LCL	UCL	% CV	LCL	UCL	% CV	%CV ($\widehat{\text{var}}_{p2}$)	Estimate	LCL	UCL
Elephant	UHR	0.063	0.003	1.401	196.3	0.019	0.213	68.3	53.5	13	1	280
Leopard (ARo)	UHN	0.05	0.033	0.069	18.0	0.031	0.080	24.4	20.1	10	7	14
Leopard (ACa)		0.069	0.045	0.093	18.1	0.046	0.103	20.8		14	9	19
Chimpanzee (ARo)	UHN	0.434	0.295	0.605	18.1	0.254	0.743	27.8	23.6	87	59	121
Chimpanzee (ACa)		0.547	0.377	0.766	18.0	0.334	0.896	25.4		109	75	153
Chimpanzee (ADO)		0.513	0.342	0.709	18.3	0.313	0.842	25.5		103	68	142
Maxwell's duiker	UHR	19.744	15.916	23.863	10.5	15.77	24.73	11.4	10.7	3949	3183	4773

Note: Also shown are %CVs of the encounter rate ($\widehat{\text{var}}_{p2}$) calculated from the raw data, and estimated population sizes (N) with bootstrap LCLs and UCLs.

† Detection function abbreviations are UHR, unadjusted hazard rate; UHN, unadjusted half-normal.

Table 4. Effects (and standard errors of effects) of the number of sampling locations and the average duration of sampling per location (in days) on the coefficient of variation of the encounter rate in camera trap distance sampling surveys of species occurring at different densities, on the inverse link scale.

Model coefficients	Maxwell's duiker	Chimpanzee
Intercept	1.529 (5.960 ⁻⁰²)	8.427 ⁻⁰¹ (4.610 ⁻⁰²)
Locations	2.490 ⁻⁰² (3.900 ⁻⁰⁴)	1.000 ⁻⁰² (3.000 ⁻⁰⁴)
Days per location	2.250 ⁻⁰² (6.900 ⁻⁰⁴)	5.700 ⁻⁰³ (4.000 ⁻⁰⁴)

increases in survey effort would have diminishing returns with respect to precision (Fig. 5).

DISCUSSION

Camera trap distance sampling shows potential to improve the efficiency and quality of inference about animal abundance from CT surveys (Howe et al. 2017, Cappelle et al. 2019, Bessone et al. 2020). Ours is only the second study to apply CTDS to multiple species or over a broad geographic scale (Bessone et al. 2020), and the first to explore relationships between spatiotemporal sampling effort and precision for species occurring at different densities and exhibiting different behaviors that affect detectability.

During our 10-month CT survey, we obtained sufficient data (minimum 60 observation of distance distributed over many locations; Buckland

et al. 2001) to estimate abundance of 31 species, including one species listed as critically endangered (western chimpanzee), two as endangered (pygmy hippopotamus and Jentink's duiker) and nine as vulnerable species (leopard, forest elephant, white-breasted guinea fowl, zebra duiker, African golden cat, and two species of primates and pangolins; IUCN red list). By comparison, Hoppe-dominik et al. (2011) were able to estimate abundances of 11 species after a 5-yr line transect survey in the same area.

For Maxwell's duikers, estimated density was similar to that reported by Hoppe-dominik et al. (2011; 17.1 ind./km² with night count) and Howe et al. (2017; 14.5–16.5 ind./km² by CTDS). Ground-dwelling, medium- to large-bodied species such as duikers are ideal subjects for CT surveys designed for estimating abundance, because their behavior, including being available for detection by CTs whenever they are active and moving, and exhibiting minimal behavioral responses to CTs, conforms well to the assumptions of statistical models (Rowcliffe et al. 2013, Howe et al. 2017, Bessone et al. 2020). Furthermore, they tend to be detected at a large fraction of random sampling locations, such that abundance can be estimated with reasonable precision (Rowcliffe et al. 2008, Nakashima et al. 2018).

As in Kouakou et al. (2009), Després-Einspinner et al. (2017), and Cappelle et al. (2019) true

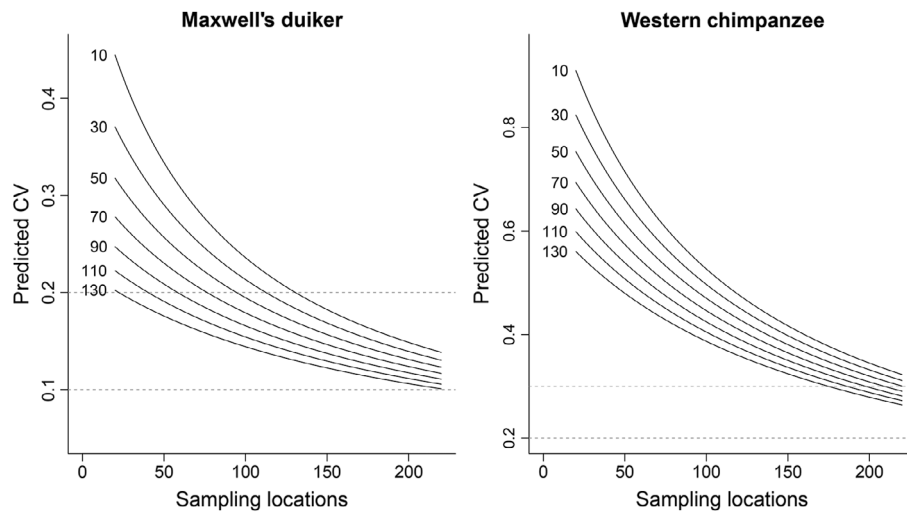


Fig. 5. Predicted coefficients of variation (CVs) of the encounter rate from camera trap distance sampling surveys of duikers and chimpanzees. Different lines show predictions for surveys of different durations (as the mean number of effective sampling days per location; labels at left).

densities of chimpanzees were known, but we sampled multiple social groups over a larger area. Camera trap distance sampling estimates were sensitive to the method used to correct for temporally availability for detection when active; we may have overestimated availability generally, possibly because there was no time at which 100% of the population was on the ground and available for detection (Rowcliffe et al. 2014, Cappelle et al. 2019). Furthermore, reactions to the camera could have caused bias either via the censoring of observations where chimpanzees were apparently reacting to CTs or effects on the distribution of observed distances (Buckland et al. 2001). By comparison, line transect distance sampling of nests either underestimated abundance (marked nest count methods) or were highly sensitive to the estimate of nest decay rate, and were no more precise than the estimates presented here, after nearly two years of active fieldwork to estimate decay rates and conduct the surveys.

Superior estimates were obtained from both 83 CTs deployed at targeted locations and 23 CTs deployed at random locations, by identifying individuals and estimating density using spatially explicit capture–recapture (SECR) methods (Després-Einspenner et al. 2017, Cappelle et al. 2019).

Estimating abundances of the rarest species by CTDS proved challenging. We obtained relatively few detections of rare elephants and leopards, and those detections were unevenly distributed in both space and time. These species also exhibited complex reactions to cameras, with effects on distributions of observed distances. Nevertheless, our estimate of 10–14 leopards on a 200-km² study area is similar to Jenny’s (1996) estimate of seven leopards on their 100-km² study area. Forest elephants occur at very low densities and move along established trails, which makes it difficult to obtain sufficient data and precise estimates from randomized surveys. Our estimate of elephant density is more than twice as high and much less precise than a prior estimate from line transect surveys over a 520-km² area that included our study area (13 individuals, 95% CI = 7–24; WCF, *unpublished report*). We also are cautious with our estimates for elephants, since they were derived from few locations, and distance sampling models did not fit our elephant data well.

The variance of the encounter rate was a reasonable proxy for the variance of density. However, our estimates of encounter rates (and therefore densities) of leopards were sensitive to sampling artifacts, that is, not the number of

locations or the average duration of sampling, but which specific locations and days were included in each data set, and therefore that we cannot reliably quantify the relative influence of different components of survey effort on the precision of CTDS estimates for species as rare as leopards and elephants. Our assessment of the relative influences of spatial and temporal survey effort on the precision of estimates of duiker encounter rates can help researchers design efficient surveys of relatively common, ground-dwelling species. Coefficients for duikers predicted a CV of the encounter rate of 27% from Howe et al.'s (2017) survey with 21 locations and a mean of 72 d of sampling per location—similar or identical to their reported analytic CVs of density. Coefficients for chimpanzees predicted a CV of 44% from Cappelle et al.'s (2019) survey with 23 locations and a mean of 206 survey days per location; they reported a bootstrap CV of 40%. When we used coefficients for duikers and chimpanzees to predict CVs from Bessone et al.'s (2020) survey with 734 locations and 36.4 sampling days per location, we obtained 5% and 12%, respectively. However, Bessone et al. (2020) did not achieve CVs lower than 20% for any species occurring at a density similar to chimpanzees on our study area, and they obtained CVs closer to 40% for semi-arboreal species. None of the species occurred at densities similar to Maxwell's duikers on our study area, but even for the most abundant and commonly detected species, CVs were >15%. Comparisons to Bessone et al. (2020) highlight the risks and uncertainty associated with predicting CVs beyond the range of our own data (maximum approximately 200 locations and 150 d per location), and is not recommended. Predictions from GLM coefficients within the range of our own data indicate that CVs between 10% and 20% of the point estimate are achievable from a wide variety of survey designs, including designs that involve moving cameras, but also that this level of precision is likely not attainable except after more than six months of sampling at a minimum of 50 sampling locations, or as little as 2–3 weeks of sampling at each of 150 or more locations.

Our results for chimpanzees, leopards, and elephants are informative regarding CTDS surveys of uncommon to very rare species that are detected rarely at randomly located CTs because

they travel along trails or spend time outside the vertical range of CTs. We suggest that crude but useful estimates of the abundance of, for example, primates, felids, and meso-carnivores could be obtained from ambitious CTDS surveys. Furthermore, if the data collected are insufficient to estimate abundance by CTDS, data collected from randomized surveys can be used to address other questions, for example, studies of occupancy and habitat use. However, if enumeration of a single or very few rare and difficult-to-detect species is the main objective of a CT survey, other methods, such as spatially explicit capture–recapture (Borchers and Efford 2008), which relies on individual identification but allows for non-random trap placement, should be considered. This might still not preclude a simultaneous multispecies CTDS survey. In some situations, identifying individuals detected by the same randomly located cameras used for a CTDS survey might be sufficient to estimate density by SECR (Després-Einspenner et al. 2017), and in others, a randomized design could be augmented with a small number of non-random sampling locations, for example, to increase detections of animals that use trails.

We conclude that CTDS could allow researchers to take advantage of the efficiency of camera trapping to obtain reliable estimates of the abundance of multiple species, of sufficient precision to detect strong trends and to inform conservation status and actions.

ACKNOWLEDGMENTS

The authors thank the Max Planck Society in Germany, The Robert Bosch Foundation, the Wild Chimpanzee Foundation, the Ministère des Eaux et Forêts, Ministère de l'Enseignement supérieur et de la Recherche scientifique, and the Office Ivoirien des Parcs et Réserves for permitting this research, as well as the Taï Chimpanzee Project. This study was conducted with the financial support of the Max Planck Society and ARCUS foundation. We thank Roger Mundry for the statistical support. We particularly want to thank Serge N'Goran for his invaluable help in supervising field and data processing assistants. We thank Alphonse, Emile, Eric, Lambert, Martin, and Nicaise for their support in fieldwork, Alejandro Estrella, Adiko Noël, Ange, Benjamin Debétencourt, Christina, Coulibaly, Daniel, Diomande, Hanna, Heather Cohen, Iko Noël, Ines, Kouadio, Lisa Orth, Amoakon et Sita Scherer for their

invaluable help in the data processing. We also want to thank Emmanuelle Normand for her support in the management of fieldwork and data processing.

LITERATURE CITED

- Anderson, D. P., E. V. Nordheim, T. C. Moermond, Z. B. G. Bi, and C. Boesch. 2005. Factors influencing tree phenology in Taï National Park, Côte d'Ivoire. *Biotropica* 37:631–640.
- Anile, S., B. Ragni, E. Randi, F. Mattucci, and F. Rovero. 2014. Wildcat population density on the Etna volcano, Italy: A comparison of density estimation methods. *Journal of Zoology* 293:252–261.
- Balestrieri, A. 2016. Distribution and ecology of lowland pine marten *Martes martes* L. 1758. Dissertation. University of Milan, Milan, Italy.
- Bessone, M., et al. 2020. Drawn out of the shadows: Surveying secretive forest species with camera trap distance sampling. *Journal of Applied Ecology* 57:963–974.
- Boesch, C., C. Crockford, I. Herbinger, R. Wittig, Y. Moebius, and E. Normand. 2008. Intergroup conflicts among chimpanzees in Taï National Park: Lethal violence and the female perspective. *American Journal of Primatology* 70:519–532.
- Boesch, C., G. Kohou, H. Néné, and L. Vigilant. 2006. Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology* 130:103–115.
- Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64:377–385.
- Buckland, S. T. 2006. Point-transect surveys for songbirds: robust methodologies. *Auk* 123:345–357.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, Oxford, UK.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, UK.
- Buckland, S. T., A. J. Plumptre, L. Thomas, and E. A. Rexstad. 2010. Design and analysis of line transect surveys for primates design and analysis of line transect surveys for primates. *International Journal of Primatology* 31:833–847.
- Burnham, K. P., and D. R. Anderson. 2002. Avoiding pitfalls when using information theoretic methods. *Journal of Wildlife Management* 66:912–918.
- Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* 52:675–685.
- Campos-Candela, A., M. Palmer, S. Balle, and J. Alós. 2018. A camera-based method for estimating absolute density in animals displaying home range behaviour. *Journal of Animal Ecology* 38:42–49.
- Cappelle, N., M. L. Després-Einspenner, E. J. Howe, C. Boesch, and H. S. Kühl. 2019. Validating camera trap distance sampling for chimpanzees. *American Journal of Primatology* 81:e22962.
- Caravaggi, A., M. Zaccaroni, F. Riga, S. C. Schai-Braun, J. T. A. Dick, W. I. Montgomery, and N. Reid. 2016. An invasive-native mammalian species replacement process captured by camera trap survey random encounter models. *Remote Sensing in Ecology and Conservation* 2:45–58.
- Chandler, R. B., and A. J. Royle. 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. *Annals of Applied Statistics* 7:936–954.
- Cusack, J. J., A. J. Dickman, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson. 2015. Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLOS ONE* 10:e0126373.
- Després-Einspenner, M. L., E. J. Howe, P. Drapeau, and H. S. Kühl. 2017. An empirical evaluation of camera trapping and spatially explicit capture-recapture models for estimating chimpanzee density. *American Journal of Primatology* 79:1–12.
- Doran, D. 1989. Chimpanzee and Pygmy chimpanzee positional behavior: the influence of environment, body size, morphology, and ontogeny on locomotion and posture. Dissertation. University of New York, New York City, New York, USA.
- Fewster, R., S. Buckland, K. Burnham, D. Borchers, P. Jupp, J. Laake, and L. Thomas. 2009. Estimating the encounter rate variance in distance sampling. *Biometrics* 65:225–236.
- Gilbert, N. A., J. D. J. Clare, J. L. Stenglein, and B. Zuckerberg. 2020. Abundance estimation of unmarked animals based on camera-trap data. *Conservation Biology* 1–12.
- Hoppe-dominik, B., H. S. Kühl, G. Radl, and F. Fischer. 2011. Long-term monitoring of large rainforest mammals in the Côte d'Ivoire Biosphere Reserve of Taï National Park, Côte d'Ivoire. *African Journal of Ecology* 49:450–458.
- Howe, E. J., S. T. Buckland, M.-L. Després-Einspenner, and H. S. Kühl. 2017. Distance sampling with camera traps. *Methods in Ecology and Evolution* 8:1558–1565.
- Hutchinson, J. M. C., and P. M. Waser. 2007. Use, misuse and extensions of “ideal gas” models of animal encounter. *Biological Reviews* 82:335–359.

- Jenny, D. 1996. Spatial organization of leopards *Panthera pardus* in Taï National Park, Ivory Coast: is rainforest habitat a 'tropical haven'? *Journal of Zoology* 240:427–440.
- Jourdain, N. O. A. S., D. J. Cole, M. S. Ridout, and J. M. Rowcliffe. 2020. Statistical development of animal density estimation using random encounter modelling. *Journal of Agricultural, Biological, and Environmental Statistics* 25:148–167.
- Karanth, K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation* 71:333–338.
- Kouakou, C. Y., C. Boesch, and H. S. Kühl. 2009. Estimating chimpanzee population size with nest counts: Validating methods in Taï National Park. *American Journal of Primatology* 71:447–457.
- Lucas, T. C. D., E. A. Moorcroft, R. Freeman, J. M. Rowcliffe, and K. E. Jones. 2015. A generalised random encounter model for estimating animal density with remote sensor data. *Methods in Ecology and Evolution* 6:500–509.
- Luo, G., W. Wei, Q. Dai, and J. Ran. 2020. Density estimation of unmarked populations using camera traps in heterogeneous space. *Wildlife Society Bulletin* 44:173–181.
- Marini, F., B. Franzetti, A. Calabrese, S. Cappellini, and S. Focardi. 2009. Response to human presence during nocturnal line transect surveys in fallow deer (*Dama dama*) and wild boar (*Sus scrofa*). *European Journal of Wildlife Research* 55:107–115.
- Marques, T., L. Thomas, S. Fancy, and S. T. Buckland. 2007. Improving estimates of bird density using multiple-covariate distance sampling. *The Auk* 124:1229–1243.
- Marshall, A. R., J. C. Lovett, and P. C. L. White. 2008. Selection of line-transect methods for estimating the density of group-living animals: Lessons from the primates. *American Journal of Primatology* 70:452–462.
- McCullagh, P., and J. Nelder. 1989. *Generalized linear models*. Chapman and Hall, London, UK.
- Moeller, A. K., P. M. Lukacs, and J. S. Horne. 2018. Three novel methods to estimate abundance of unmarked animals using remote cameras. *Ecosphere* 9:e02331.
- Nakashima, Y., K. Fukasawa, and H. Samejima. 2018. Estimating animal density without individual recognition using information derivable exclusively from camera traps. *Journal of Applied Ecology* 55:735–744.
- Nakashima, Y., S. Hongo, and E. F. Akomo-Okoue. 2020. Landscape-scale estimation of forest ungulate density and biomass using camera traps: Applying the REST model. *Biological Conservation* 241:108381.
- Nichols, J. D., and B. K. Williams. 2006. Monitoring for conservation. *Trends in Ecology and Evolution* 21:668–673.
- Rovero, F., and A. R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* 46:1011–1017.
- Rovero, F., M. Tobler, and J. Sanderson. 2010. Camera trapping for inventorying terrestrial vertebrates. Pages 100–128 *in* Manual on field recording techniques and protocols for all taxa biodiversity inventories and monitoring. The Belgian National Focal Point to the Global Taxonomy Initiative.
- Rovero, F., and F. Zimmermann. 2016. *Camera trapping for wildlife research*. Pelagic Publishing, Exeter, UK.
- Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* 45:1228–1236.
- Rowcliffe, J. M., P. A. Jansen, R. Kays, B. Kranstauber, and C. Carbone. 2016. Wildlife speed cameras: measuring animal travel speed and day range using camera traps. *Remote Sensing in Ecology and Conservation* 2:84–94.
- Rowcliffe, J. M., R. Kays, C. Carbone, and P. A. Jansen. 2013. Clarifying assumptions behind the estimation of animal density from camera trap rates. *Journal of Wildlife Management*. <https://doi.org/10.1002/jwmg.533>
- Rowcliffe, J. M., R. Kays, B. Kranstauber, C. Carbone, and P. A. Jansen. 2014. Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution* 5:1170–1179.
- Rowcliffe, M. J., C. Carbone, P. A. Jansen, R. Kays, and B. Kranstauber. 2011. Quantifying the sensitivity of camera traps: An adapted distance sampling approach. *Methods in Ecology and Evolution* 2:464–476.
- Si, X., R. Kays, and P. Ding. 2014. How long is enough to detect terrestrial animals, estimating the minimum trapping effort on camera traps. *PeerJ* 2:e374.
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47:5–14.
- Tiedoué, M. R., A. Diarrassouba, and A. Tondossama. 2016. Etat de conservation du Parc national de Taï: Résultats du suivi écologique, Phase 11. Office

- Ivoirien des Parcs et Réserves/Direction de Zone Sud-ouest, Soubré, Côte d'Ivoire.
- WCF. 2016. Rapport annuel de 2016. https://www.wildchimps.org/fileadmin/content_files/pdfs/reports/2017_WCF_Rapport_annuel_final_FR_2016_30-05-2017.pdf
- Zero, V. H., S. R. Sundaresan, T. G. O'Brien, and M. F. Kinnaird. 2013. Monitoring an endangered savannah ungulate, Grevy's zebra *Equus grevyi*: Choosing a method for estimating population densities. *Oryx* 47:410–419.