

RESEARCH ARTICLE

Validating camera trap distance sampling for chimpanzees

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Abstract

The extension of distance sampling methods to accommodate observations from camera traps has recently enhanced the potential to remotely monitor multiple species without the need of additional data collection (sign production and decay rates) or individual identification. However, the method requires that the proportion of time is quantifiable when animals can be detected by the cameras. This can be problematic, for instance, when animals spend time above the ground, which is the case for most primates. In this study, we aimed to validate camera trap distance sampling (CTDS) for the semiarboreal western chimpanzee (*Pan troglodytes verus*) in Taï National Park, Côte d'Ivoire by estimating abundance of a population of known size and comparing estimates to those from other commonly applied methods. We estimated chimpanzee abundance using CTDS and accounted for limited availability for detection (semiarboreal). We evaluated bias and precision of estimates, as well as costs and efforts required to obtain them, and compared them to those from spatially explicit capture-recapture (SECR) and line transect nest surveys. Abundance estimates obtained by CTDS and SECR produced a similar negligible bias, but CTDS yielded a larger coefficient of variation (CV = 39.70% for CTDS vs. 1%/19% for SECR). Line transects generated the most biased abundance estimates but yielded a better coefficient of variation (27.40–27.85%) than CTDS. Camera trap surveys were twice more costly than line transects because of the initial cost of cameras, while line transects surveys required more than twice as much time in the field. This study demonstrates the potential to obtain unbiased estimates of the abundance of semiarboreal species like chimpanzees by CTDS.

HIGHLIGHTS

- Camera trap distance sampling produced accurate density estimates for semi-arboreal chimpanzees.
- Availability for detection must be accounted for and can be derived from the activity pattern.

KEYWORDS

animal survey, comparative evaluation, monitoring, *Pan troglodytes verus*, spatial-explicit capture-recapture

1 | INTRODUCTION

Wildlife is increasingly threatened due to human impact despite significant conservation actions around the world (World Wide Fund for Nature, 2018). For effective conservation and successful management, there is a need for efficient monitoring tools that reliably and precisely estimate wildlife population sizes and their trends over time (Plumptre & Cox, 2006). Yet, a popular statistical method to estimate the abundance and density of wild animal populations, distance sampling, might fail to monitor elusive species because they tend to avoid human observers during field surveys, which creates biases in estimates (Buckland et al., 2001; Buckland, Plumptre, Thomas, & Rexstad, 2010; Buckland, Rexstad, Marques, & Oedekoven, 2015; Rovero & Marshall, 2004). To overcome this problem, indirect observations such as dung and nest counts can be recorded. However, estimates of sign production and decay rates are then required to convert estimates of sign density into estimates of animal density. These auxiliary variables are often difficult to obtain and often imprecisely estimated (Buckland et al., 2001; Kuehl, Todd, Boesch, & Walsh, 2007; Kühl, Maisels, Ancrenaz, Williamson, & Williamson, 2008; Plumptre & Reynolds, 1996; Walsh & White, 2005).

Recent technological developments, including camera traps, provide new methods to monitor wildlife. Camera traps are very efficient for detecting elusive and rare species in remote habitats (Burton et al., 2015; Rovero & Zimmermann, 2016; Silveira, Jácomo, & Diniz-Filho, 2003). Where individuals can be identified from images or videos, capture-recapture methods can be used to estimate abundance accurately and precisely (Després-Einspenner, Howe, Drapeau, & Kühl, 2017; Head et al., 2013; Karanth, 1995; Karanth, Nichols, Kumar, & Hines, 2006; Silver et al., 2004; Soisalo & Cavalcanti, 2006; Trolle & Kery, 2005).

However, species without individual markings have been under-represented in past camera trapping research (Burton et al., 2015). To address this gap, a method for estimating animal abundance by distance sampling with camera traps (CTDS) has been recently developed (Howe, Buckland, Després-Einspenner, & Kühl, 2017). This technique uses camera traps in lieu of human observers at point transects by treating observations as a series of snapshots. This approach has the advantage of excluding human interference from the observation process. In addition, the cameras continuously record observations of animals 24 hr/day.

However, this method requires that the total amount of time that animals are available for detection by the cameras during a survey is known or quantifiable. This may be the case for terrestrial species that can be assumed to be available for detection during the defined daily survey period (Howe et al., 2017). In the case of chimpanzees, the availability for detection can be defined as time spent on the ground. Most primates are semiarboreal, so they are only available for detection when they are both active and within the vertical range of camera traps.

In this study, we aimed to (a) validate the CTDS approach by applying it to a chimpanzee group of known size, (b) estimate

availability for detection to account for the semiterrestriality, (c) compare the bias and precision of this method with estimates from line transect nest count sampling and spatially explicit capture-recapture (SECR), and (d) inform chimpanzee monitoring programs by identifying the most cost-effective method for estimating chimpanzee densities.

2 | METHODS

2.1 | Study site

Data were collected in Taï National Park, Côte d'Ivoire (5°08'N to 6°407'N, and 6°47'W to 7°25'W), from June 2014 to March 2015. This park is one of the largest remaining tracts of undisturbed lowland rain forest in West Africa, spreading over 5,400 km². Average annual rainfall is approximately 1,800 mm and the annual average temperature is between 24 and 30°C (Anderson, Nordheim, Moermond, Bi, & Boesch, 2005). In the western area of the park, four groups of chimpanzees (the "North," "Middle," "South," and "East" groups) have gradually been habituated to humans over several years (Boesch et al., 2008; Boesch, Kohou, Néné, & Vigilant, 2006; Kouakou, Boesch, & Kühl, 2009). These groups have been followed on a daily basis with GPS devices and, therefore, abundance and territory sizes were known.

2.2 | DATA COLLECTION

2.2.1 | Camera traps survey

A total of 23 video cameras (Bushnell Trophy Cam™; Model #119576C; <http://bushnell.com>) were installed across the territory of the East group over a 10-month period (Figure 1). Motion detectors were programmed to trigger as soon as movement was detected, set to high sensitivity, and active 24 hr/day. When triggered, cameras recorded only 60 s of the video. The cameras were placed systematically within 30 meters of the intersections of a 1 × 1 km grid with random origin. Each camera was oriented approximately toward the geographic north to avoid backlight, with a variation of ±40° to allow sufficient visibility (e.g., to avoid placing a camera in front of a large trunk, but without targeting placement to increase detection probability) and at a height of 0.75–1 meters from the ground. Two cameras were moved (<3 meters) during the study period, because of termites infesting the camera and a leopard attacking one of the cameras, thus there were a total of 25 sampling locations. At each location, reference videos were recorded by holding distance labels at predefined distances (from 1 to 15 meters at 1-meter intervals, in the center, and at each side of the camera's field of view) so that we could subsequently estimate observation distances to animals moving in front of the camera (see Howe et al., 2017 for details).

All individuals of the East group were previously identified in camera trap footage for the purposes of estimating abundance using SECR (Després-Einspenner et al., 2017). Results from the set of systematically-placed cameras (i.e., the same ones used for the SECR

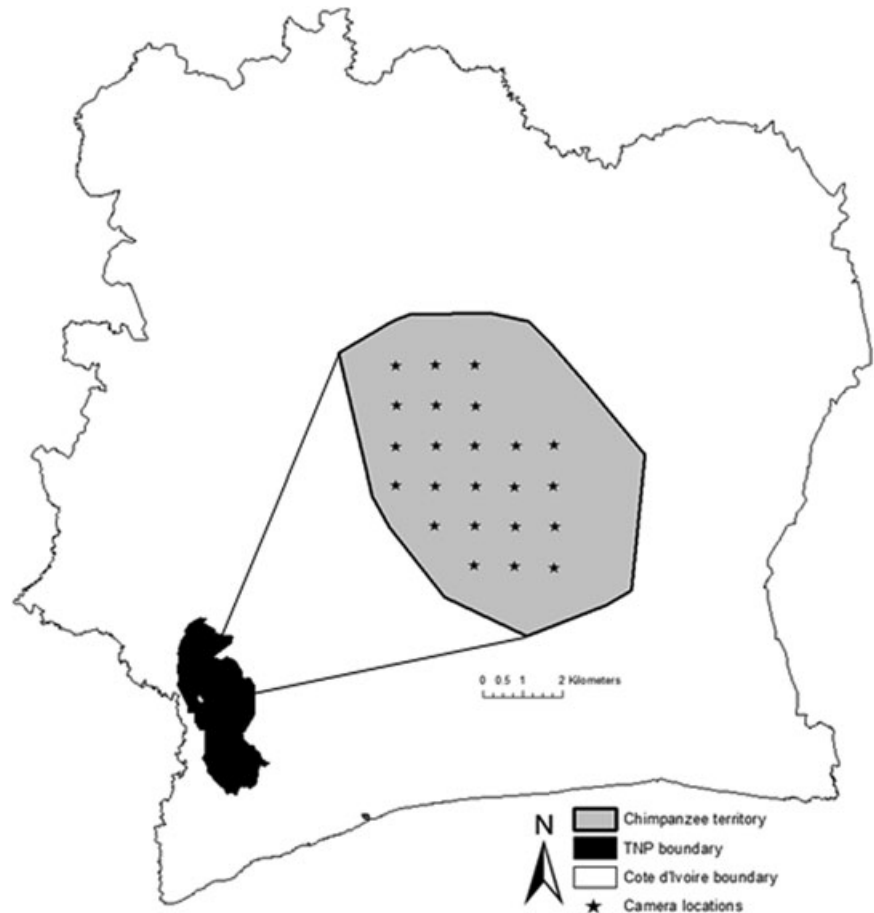


FIGURE 1 Location of cameras in the East chimpanzee group territory in the Tai National Park (TNP)

analysis in Després-Einspenner et al., 2017) are presented here for comparison with CTDS results. Després-Einspenner et al. (2017) estimated standard errors (SEs) and associated coefficients of variation (CVs) around densities estimated from SECR models under the assumption that the number of activity centers was binomially distributed, which was appropriate because all traps were intentionally located within the territory of a single group. For the sake of comparisons of precision with other methods, we re-estimated the SE and CV under the assumption that the number of activity centers was Poisson-distributed, as would be the case if unhabituated populations were sampled over a larger area, because territory boundaries would be unknown.

The size of the territory of the East group was used to convert estimates of density to estimates of population size (Després-Einspenner et al., 2017).

2.2.2 | Line transect surveys

We used results from an intensive line transect distance sampling survey of nests conducted between June 2004 and May 2006 by Kouakou, Boesch, and Kuehl (2009) for comparison with CTDS and SECR results. Line transects were spread over three well known and habituated groups (North, South, and East) in the Tai National Park (for more details see Kouakou et al., 2009).

Because knowing the nest decay rate is mandatory to obtain reliable abundance estimates from line transects (Buckland 2001; Kühl et al., 2008), a nest decay survey was conducted in the first year of the study, and the actual line transects survey in the second year. Density and population size were estimated using two different methods (marked nest count and standing-crop nest counts), which resulted in two estimates of density and population size.

2.3 | DATA ANALYSIS

2.3.1 | Availability for detection

Chimpanzees spend their nights in tree nests, thus they are unavailable for detection by camera traps during the nesting period. In addition, they are unavailable for detection when active in the trees during the daytime. To account for this nonavailability, we estimated the proportion of time when chimpanzees are available for detection by the cameras. We used the number of videos of chimpanzees obtained per hour as a proxy for the proportion of time chimpanzees was on the ground. We assumed that at the peak of their activity (maximum number of videos per 1-hr interval; see Figure 2), all chimpanzees would be available for detection on the ground. If all chimpanzees or the populations surveyed are not available for detection during their peak of activity, temporal sampling effort would be overestimated, and consequently, density

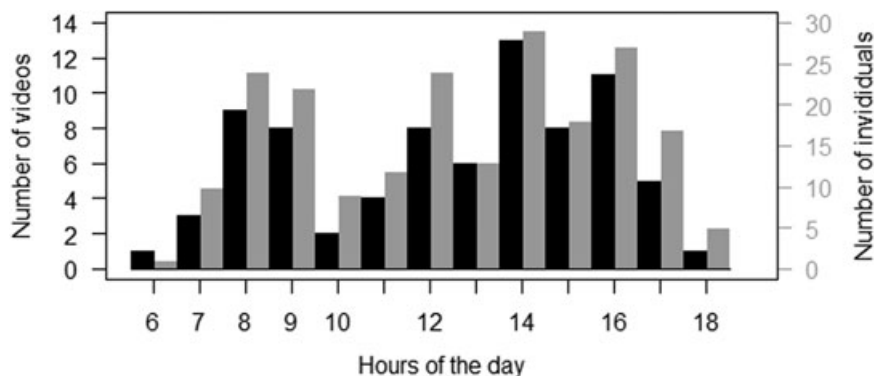


FIGURE 2 Number of videos of chimpanzees (in black) and number of individuals seen (in gray) each hour for the entire survey period

estimates would be negatively biased; bias would be proportional to the fraction of the population not available for detection during peak activity (if 90% were active, we expect underestimation of true density by 10%).

We then calculated the proportion of time chimpanzees spend on the ground using the following equation:

$$A = \frac{n_T}{T_i \times n_p} \quad (1)$$

where A is the proportion of time spent on the ground during the day (hereafter “availability”), T_i is the number of 1-hr intervals when chimpanzees were actually active (not nesting), n_p is the number of videos obtained at peak of activity, and n_T is the total number of videos of chimpanzees. We used this proportion of time spent on the ground as “availability” to correct the naïve population size and density estimates obtained under the assumption that chimpanzees were always available for detection.

Furthermore, we compared our estimate of availability derived from the camera trap data to data from a previous study using direct observations of chimpanzees in the same area (Doran, 1989). In this study, time spent on the ground was provided separately for males and females. We adjusted these results to our study group by taking the percentage of time spent on the ground by males and females multiplied by the proportion of male and female individuals in the group (all juveniles and infants were included with the females, as they are in the constant presence of the mother).

2.3.2 | True abundance of chimpanzees during the surveys

At the time of the camera trap study, there were 36 individuals (including 27 individual noninfants aged >4 years) in the East group (long-term database Taï chimpanzee project). At the time of the line transect survey (Kouakou et al., 2009), there were 40 weaned individuals in the three habituated groups (North, Middle, and South).

The true density was calculated by dividing the true abundance by the territory size.

2.3.3 | Distance sampling with camera traps

We recorded observation distances between cameras and the midpoints of each filmed chimpanzee at 2-s intervals (i.e., at 0, 2, 4, ..., 58 s after the start of the video), independent of whether single individuals or groups were seen. The distances between cameras and individual chimpanzees were derived by comparing their locations to those of the distance labels in the reference videos. Animals were assigned to 1-meter distance intervals from 0 to 8 meters. Because precise distances are more difficult to assess for objects further away from the camera, observations over 8 meters were assigned to one of the following categories: 8–10 m, 10–12 m, 12–15 m, and beyond 15 m. Following exploratory analyses (Buckland et al., 2001, Marques et al., 2007), we left-truncated the data at 2 meters and right-truncated it at 15 meters before estimating abundance.

Chimpanzee density was estimated using Distance 7.0 (Thomas et al., 2010) with the following equation for camera trap point transects:

$$\hat{D} = \frac{n_k}{\pi w^2 e_k \hat{P}_k} \times \frac{1}{A} \quad (2)$$

where $e_k = \frac{\theta T_k}{2\pi t}$ is the sampling effort at point k , T_k is the total sampling time 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 so that $\frac{\theta}{2\pi}$ is the proportion of the full circle covered by the field of view of the camera, w is the truncation distance, beyond which any recorded distances are discarded, n_k is the number of observations of distances to chimpanzees at point k , and \hat{P}_k is the estimated probability that a chimpanzee is detected by the sensor and an image obtained when within the field of view of the camera at a snapshot moment as estimated by the modeled detection function (Howe et al., 2017), and $\frac{1}{A}$ is the availability correction factor (see Equation 1). We estimated population size by multiplying the density estimate by the territory size.

Temporal effort at each point (T_k) excluded the 11-hr nighttime interval (19:00:00–5:59:59) when chimpanzees were expected to be in their nests and during that time no videos of chimpanzees were recorded. Therefore, T_k was calculated as the number of seconds

from 6:00:00 through 18:59:59 multiplied by the number of camera days per point. Effort data from one camera was excluded from the analysis because it was located on a steep slope and thus did not provide an opportunity to detect animals. Likewise, effort data from 464 camera days from eight cameras were excluded because of technical problems (SD cards or cameras not functioning, or camera missing when revisited), or because of leaves stuck on the camera lens, prohibiting a clear view of the field in front of the camera. Finally, effort data and distance observations from days when cameras were installed or visited by researchers were excluded to avoid any potential bias created by the researchers' presence.

We considered CTDS models with half-normal and hazard rate key functions with no adjustment terms, and a uniform key function with one cosine adjustment term. Because observations were not independent, we estimated variances from 999 nonparametric bootstrap resamples of data from the different points (Buckland et al., 2001). Furthermore, rather than selecting the AIC-minimizing model for estimation, we calculated abundances and CVs as the AIC-weighted average across all fitted models (Wagenmakers & Farrell, 2004).

2.3.4 | Comparison of methods

First, we calculated relative bias of estimates from all the methods relative to the known true densities to determine the ability of methods to give reliable estimates with the following equation:

$$\text{Relative bias} = \frac{(\hat{D} - D)}{D} \quad (3)$$

where \hat{D} is the estimated density and D is the known true density.

We compared CVs among the estimates to assess their relative precision. They were calculated with the following equation:

$$\text{CV}(\hat{D}) = \frac{\hat{se}(\hat{D})}{\hat{D}} \quad (4)$$

where $\hat{se}(\hat{D})$ is the SE of the estimated density \hat{D} .

Then, we determined equipment costs, manpower, and analysis time for each method. Material costs for SECR and point transect methods include cameras and all the material needed to maintain function (e.g., batteries, SD cards) and to move through the forest (e.g., GPS). Those for the line transect method include costs and effort from the line transect survey as well as for the studies on nest production and decay rate surveys.

TABLE 1 Results for CTDS: Population size, confidence intervals of population size, density, confidence intervals of density, coefficient of variation, Akaike information criterion, Δ_i (AIC) ($=[\text{AIC}_i - \min(\text{AIC})]$), and the rounded Akaike weights estimated for each different model (hazard rate and half normal with no adjustment terms and uniform with 1 cosine adjustment term)

Model	N	NCI	D	DCI	CV	Δ_i (AIC)	W_i (AIC)
Hazard rate	34	12–72	0.838	0.308–1.792	0.430	0.00	0.58
Half normal	38	15–68	0.933	0.382–1.676	0.360	1.78	0.24
Uniform	40	15–70	0.996	0.382–1.743	0.343	2.27	0.19

Note. AIC: Akaike information criterion; CTDS: camera trap distance sampling; CV: coefficient of variation; D, density; DCI, confidence intervals of density; N: population size; NCI: confidence intervals of population size; $w_i(\text{AIC})$: rounded Akaike weights

This study adhered to the American Society of Primatologists principles for the ethical treatment of primates. Field protocols, data collection, and data analysis were conducted in accordance with wildlife research protocols and ethical standards of the Max Planck Society in Germany, the Center Suisse de Recherches Scientifiques, the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique, and the Ministère de l'Environnement et des Eaux et Forêts in Côte d'Ivoire.

3 | RESULTS

3.1 | Territory size and known group density

The size of the territory of the East group was 40.37 km². Detections of infants were excluded from the SECR data because infant–mother pairs were always captured together and SECR models assume independent detections (conditional on activity center). Therefore, the known chimpanzee density for the group, which was used to compare with SECR estimates, included only weaned individuals ($N = 27$), and was 0.67 individual/km².

For CTDS, infants were included in the analysis as there was no need for individual recognition, and the assumption of independence was already severely violated because we recorded distances to the same animals multiple times during a single independent encounter (Howe et al., 2017). The known chimpanzee density for the entire group used for comparison with point transects estimates was thus 0.89 individual/km².

3.2 | Availability for detection

We recorded a total of 81 videos of chimpanzees during the survey. All videos were recorded between 6:00:00 and 18:59:59 hr (Figure 2). The peak of activity inferred from the hourly numbers of videos recorded and the number of individuals seen occurred between 14:00 and 15:00, when 13 videos were recorded (Figure 2). Following Equation 1, chimpanzees spent 48% of their time on the ground during the 13-hr daytime interval. Thus, the availability (A) was 0.48.

When using the time chimpanzees spent on the ground during daytime established in by Doran (1989) (males and females spent 66.2% and 46.9% of time on the ground, respectively) and adjusting to the demographic structure of our group, we estimated that chimpanzees spent 49.6% of their time on the ground.

TABLE 2 Estimation of density (\hat{D}), population size (\hat{N}), confidence intervals of population size $\hat{N}CI$, percentage of coefficient of variation (% CV) and relative bias (%) is given for each different technique. The real number of individuals in the group with the related density (N and D , respectively) is also given for each technique

Techniques		D and N	\hat{D}	\hat{N}	$\hat{N}CI$	CV, %	Relative bias, %
Point transects	Weighted AIC	0.89–36	0.89	36.06	13.27–70.68	39.70	0.2
Line transects	Marked nest counts	0.89–40	0.84	37	22–64	27.40	–7.5
	Standing-crop nest counts		0.78	35	20–60	27.85	–12.5
SECR	Complete subset of data	0.67–27	0.66	27.07	26.55–27.59	1.00 (19.00) ^a	0.3

Note. AIC: Akaike information criterion; CI: confidence interval; CV: coefficient of variation.

^aCV yielded under the assumption that the number of activity centers was Poisson-distributed.

3.3 | Emporal sampling effort (t_k) and sample sizes

Survey effort represented a total of 4,731 camera trap days. Of the 81 videos of chimpanzees recorded, there were a total of 364 detections of individual chimpanzees (including weaned individuals and infants), which resulted in 2,116 extracted distance observations. Left-truncating the data at 2 meter and right-truncating at 15 meter reduced the data to 2,001 observations. About 65% of these observations came from three cameras (two were on trails and one near a fruiting tree [*Irvingia gabonensis*]). No chimpanzees were detected at six of the 22 cameras.

3.4 | Abundance estimation

All point transect models yielded reasonable density estimates after correcting for temporally limited availability for detection (Table 1). The AIC-weighted average estimate was 0.89 individuals/km²; multiplying by the territory size yielded a population estimate of 36.06 individuals (Table 2).

Abundances estimated by SECR were accurate, and those estimated from line transect surveys of nests were reasonably accurate (Table 2).

3.5 | Comparison of effort-precision between different methods

SECR and CTDS yielded the most accurate estimates, and CTDS yielded the least precise estimate (Table 2). Methods using camera traps were the most expensive because of the primary cost of cameras. The duration of the SECR fieldwork was the same as for the CTDS study, because both were conducted as part of the same field survey and using the same cameras. Recording all the distance observations for CTDS was relatively fast (about 2 weeks) because of the low number of videos but took longer than identifying individual chimpanzees as they were all well known to researchers.

The line transects method was the least expensive, and because of the nest decay study, the most time consuming in the field (Table 3).

4 | DISCUSSION

This is the first study evaluating the efficacy and applicability of CTDS for the monitoring of a semiarboresal species. We have shown that CTDS in combination with an estimate of availability can yield accurate estimates. Point transect surveys require randomized designs (including systematic designs with random origin), and the precision of abundance estimates is largely a function of the variation in encounter rate among sampling locations (Buckland et al., 2001). The fact that most observations were obtained at only three cameras explains the imprecision of these estimates and highlights the importance of sampling at more locations to improve precision (also see Cappelle et al. in prep).

4.1 | Availability for detection

As semiarboresal species spend some time outside the field of view of cameras, it was critical to quantify availability for detection when estimating chimpanzee abundance by CTDS (Howe et al., 2017). The percentage of time chimpanzees spent on the ground during the day estimated from our camera-trapping data was very similar to what has been directly observed (Doran, 1989). This suggests, therefore, that our estimate of availability was a good approximation and that temporal distribution of videos reflect the time chimpanzees spend on the ground. Availability for detection may vary from site to site, as is the case for nest and dung production and decay rates (Kouakou

TABLE 3 Equipment costs (in Euro), salaries of local assistants needed for fieldwork only, time (in days) spent in the field and time (in days) to analyze data for each technique (time for processing all the data and to obtain decay and production rates, density and population size estimates). All the data for line transects are for the two-year survey in the East chimpanzee group

Technique	Equipment costs (€)	Assistant salaries (€)	Days in the field	Time of analysis (days)
Point Transect	5380	322	94	100
SECR	5380	322	94	90
Line Transect	730	2089	238	60

et al., 2009; Kuehl et al., 2007; Plumptre & Reynolds, 1996; Walsh & White, 2005). For example, chimpanzees could spend more time on the ground in more open habitats. Survey-specific estimates should, therefore, be calculated from each CTDS survey conducted. Furthermore, the concordance between estimates of time spent on the ground from camera trapping and direct observations should be tested and validated for other chimpanzee populations where possible. Information about time spent on the ground and in trees is available from other long-term study sites and would facilitate comparisons with estimates of availability from camera trap data.

4.2 | Behavioral responses and data truncation

Howe et al. (2017) suggested left-truncation might be required generally with CTDS data to avoid bias associated with missed detections close to the camera (suggesting three possible mechanisms). Our data, however, included more observations than expected between 0 and 1 meter. We suspect this was because some chimpanzees stayed near the cameras for extended periods of time to touch or inspect them. This behavior is also common in other chimpanzee populations, even when not habituated to human presence (Kalan et al., in press). Attraction to or avoidance of the cameras is expected to induce bias (Buckland et al., 2001). In our case, left-truncating to ensure a reasonable fit to the detection function may also have reduced effects of behavioral responses to the cameras on the data collected and, therefore, any resulting bias to the estimated abundance.

4.3 | Validating distance sampling using camera traps for monitoring chimpanzees

CTDS yielded an exceptionally accurate estimate of chimpanzee density, demonstrating the potential of the method for efficient monitoring of chimpanzee populations. Furthermore, because CTDS simply extends distance sampling methods to camera traps, other theoretical extensions (such as the potential to model variation in abundance or detectability using covariates) could be included in more complex analyses using freely-available software, and with advice from experts (www.distancesampling.org). However, estimates were imprecise, such that it would likely be difficult to statistically demonstrate trends in abundance. This imprecision was attributable to the small number of sampling locations and the heterogeneous distribution and nonrandom movements of the chimpanzees, leading to a large variance in the encounter rate among locations (Herbinger, Boesch, & Rothe, 2001). This problem, however, can be overcome by increasing the number of sampling locations.

Furthermore, an extensive trail network is intentionally maintained within the territories of these habituated groups to facilitate focal follows. Our study design was randomized (a systematic grid with random origin). Even though two cameras fell on trails and yielded a large proportion of our total observations, it is reasonable to assume that trails were sampled proportionally to their availability

on the study area (Buckland et al., 2001). However, the trail network may have increased the nonrandomness of chimpanzee movements, further exacerbating the variation in the number of observations between camera locations, with adverse effects on precision. Distance sampling designs must be randomized, and movements will usually be nonrandom, so we recommend future surveys include more sampling locations to improve precision and consequently, making it easier to detect population changes. This could be achieved by increasing the number of cameras deployed, or, to avoid large increases in equipment costs, by moving cameras between locations during the survey.

4.4 | Comparison of techniques and implication in conservation

SECR yielded the most precise estimates, while CTDS provided equally unbiased estimates, but with a higher coefficient of variation. It is worthwhile to note that Després-Einspinner et al. (2017) assumed that the number of individual activity centers was binomially distributed when estimating the variance of the density estimate, as was appropriate because all traps were intentionally located within the territory of a single group (Borchers & Efford, 2008). In surveys of unhabituated groups where territory boundaries are unknown, the binomial distribution would be replaced by a Poisson distribution, and a spatially unconditional variance would be estimated, which would reduce precision (Borchers & Efford, 2008). For the sake of comparison, we estimated the unconditional variance and associated CV from the same SECR model fit to the same data, and obtained a CV of 0.19, much more similar to, but still lower than, CVs from other methods.

The line transect survey of nest yielded a smaller coefficient of variation, but estimates were less accurate than those obtained by either of the methods that used data from camera traps.

Comparing the costs of materials and time required to complete the validation surveys revealed that line transects sampling was the least expensive but the most time-consuming method. SECR and CTDS were more expensive but required less field time (Table 3). Overall, camera trap approaches were more expensive because of the need to acquire cameras, but involved fewer assistants for less time than line transects and were, therefore, a cheaper alternative in terms of staff cost. In addition, once cameras are bought, they can be reused in future surveys (with no or minimal additional materials costs), while money spent on staff would need to be spent again. However, in this study, the cost of data analysis has not been taken into account, so the salaries represent only the amount of money needed to hire local assistants to help with the fieldwork. The cost of analyzing videos, if in large number, could largely increase the assistant salaries for both SECR and CTDS. Automated video analysis methods for species recognition have mainly been developed with still images (e.g., Yu et al., 2013). However, new approaches for classification of species in videos are under development and will expand the opportunities for automated processing of camera trap field data. Eventually, these new approaches will save a lot of time

and money in the near future. Line transects turned out to be very time consuming in the field because of the additional need to conduct the decay and production rate studies concurrently with the line transect survey. Processing data for CTDS was slightly more time consuming than for SECR because the survey was conducted in an area where the chimpanzees were familiar to researchers and, therefore, quickly identified. Field labor of CTDS was also more intense compared to SECR, because the researchers needed to measure distances and record reference videos at each camera to facilitate estimation of distances to animals. Consequently, the SECR validation survey provided the most precise and unbiased estimates with the least time involved in the field and in data processing, while the line transect survey of nests yielded the most biased estimates for the largest amount of time spent.

5 | CONCLUSION AND FUTURE RECOMMENDATION

This study showed that CTDS can provide unbiased abundance estimates for a semiarborescent species. SECR yielded the most precise estimates, yet each method considered in this study can be useful depending on the survey duration (long-term or short-term study) and the resources available. More generally, if only one species is targeted, and individuals are easily identifiable, SECR modeling should be chosen, whereas species whose individuals are more difficult to identify should be monitored with CTDS. Alternatively, line transects should be used to monitor arboreal primates that spend little time on the ground because camera traps have not been proven effective for these species yet. Monitoring programs using camera traps initially incur high costs; yet, they require less effort and are less time consuming than line transects in the field. Data processing will be expected to be less arduous in the future, thanks to recent technological development in automation of video selection and species identification (Brust et al., 2017; Cruncheon et al., 2017; Freytag, Rodner, Darrell, & Denzler, 2014; <https://zamba.drivendata.org/>). Estimation of distances from paired cameras is straightforward (Mrovlje & Vrancic, 2008; Tjandranegara, 2005) and its application to observation distances from camera traps is under development (Kühl et al., 2008). All of these techniques could also be implemented simultaneously as part of a large multi-species survey, as the data provided by camera traps with a systematic design can be used for both SECR and CTDS, and line transects can be added while reaching the cameras.

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