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Summary

1. Reliable estimates of animal density and abundance are essential for effective wildlife conservation and management. Camera trapping has proven efficient for sampling multiple species, but statistical estimators of density from camera trapping data for species that cannot be individually identified are still in development.

2. We extend point-transect methods for estimating animal density to accommodate data from camera traps, allowing researchers to exploit existing distance sampling theory and software for designing studies and analyzing data. We tested it by simulation, and used it to estimate densities of Maxwell's duikers (*Philantomba maxwellii*) in Taï National Park, Côte d'Ivoire.

3. Densities estimated from simulated data were unbiased when we assumed animals were not available for detection during long periods of rest. Estimated duiker densities were higher than recent estimates from line transect surveys, which are believed to underestimate densities of forest ungulates.

4. We expect these methods to provide an effective means to estimate animal density from camera trapping data and to be applicable in a variety of settings.

Keywords: animal abundance, camera trapping, density, distance sampling, Maxwell's duiker

Introduction

Remote motion-sensitive photography, or camera trapping, is increasingly used in wildlife research, and allows multiple research objectives to be addressed (Sollmann et al. 2013*a*, Burton et al. 2015, Rovero and Zimmermann 2016). Estimation of population density (D) is a key objective of many ecological studies and assessments of conservation status employing

camera traps (Burton et al. 2015, Rovero and Zimmermann 2016). If individuals are recognizable, density can be estimated using spatially explicit capture–recapture (SECR) models (Efford et al. 2009), but methods for estimating *D* from camera trapping data in the absence of individual identification are still in development (Sollmann et al. 2013*a*, Burton et al. 2015, Dénes et al. 2015, Rovero and Zimmermann 2016). Detection rates at camera traps have been used to index abundance, but indices can rarely be converted to estimates of absolute density, and spatiotemporal variation in detection rates does not provide reliable evidence of differences or trends in abundance (Sollmann et al. 2013*b*, Burton et al. 2015). The random encounter model (REM) estimates absolute density as a function of the detection rate, the dimensions of a sector within which detection is certain, and the speed of animal movement; methods for quantifying the latter two parameters from camera trapping data have been described (Rowcliffe et al. 2008, 2011, 2016). The REM has been recognized as a potentially useful model, but its accuracy and reliability remains to be demonstrated (Rovero and Marshal 2009, Sollmann et al. 2013*a*, Zero et al. 2013, Cusack et al. 2015*a*, Balestrieri et al. 2016, Caravaggi et al. 2016). SECR estimators for unmarked populations estimate the number and location of animals' activity centers from the spatial correlation of counts at different sampling locations; sampling must be sufficiently intensive to detect the same animals at multiple locations, and estimates lack precision (Chandler and Royle 2013).

Here we describe how densities of unmarked animal populations can be estimated by distance sampling (DS) with camera traps, allowing researchers to take advantage of a well-described theoretical framework complete with software and advice for designing studies and analyzing data (Buckland et al. 2001, 2004, 2015, Thomas et al. 2010, Miller 2015, distancesampling.org). Below, we formulate a point transect distance sampling model specific to

camera traps and describe its assumptions and the estimation of variances. We test for bias in estimated density ($\widehat{D}$) and its variance by simulation, and apply the method to estimate the density of Maxwell's duikers (*Philantomba maxwellii*) in Taï National Park, Côte d'Ivoire.

Methods

Formulation of the Model

A camera trap (CT) is deployed at a point k that is independent of animal density for a period of time T_k and set to record images for as long as an animal is present to trigger it. We predetermine a finite set of snapshot moments within T_k, t units of time apart, at which an image of an animal could be obtained. Temporal effort at the point is then T_k / t. When images of animals are obtained, we estimate the horizontal radial distance r_i between the midpoint of each animal and the camera, at each snapshot moment, for as long as it remains in view. If the camera covers an angle θ radians, then $\frac{\theta}{2\pi}$ describes the fraction of a circle covered by the camera, so we define overall sampling effort at point k as $\frac{\theta T_k}{2\pi t}$. We regard the data as a series of snapshots, and density estimation follows by standard point transect methods (Buckland et al. 2001). We estimate D as

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

where $e_k = \frac{\theta T_k}{2\pi t}$ is the effort expended at point k, K is the set of points, θ is the horizontal angle of view (AOV) of the camera, w is the truncation distance beyond which any recorded distances are discarded, n_k is the number of observations of animals in the population of interest at point k, and $\hat{P}_k$ is the estimated probability of obtaining an image of an animal that is within θ and w in front of the camera at a snapshot moment.

. Substituting e_k in (1), we have

$$\widehat{D} = \frac{2t\sum_{k=1}^{K} n_k}{\theta w^2 \sum_{k=1}^{K} T_k \hat{P}_k} \quad (2)$$

We use the distances r_i to model the detection function and hence to estimate P_k.

Assumptions and Practical Considerations

The usual DS assumptions apply (see Chapter 2 of Buckland et al. 2001). We record distances at instantaneous snapshot moments to ensure that animal movement does not bias the distribution of detection distances. Below, we describe an approach for accurately assigning animals to distance intervals; Rowcliffe et al. (2011) and Caravaggi et al. (2016) describe methods for measuring continuous distances between CTs and detected animals.

Random designs or systematic designs with random origin are consistent with the assumption that points are placed independently of animal locations. Selecting camera orientations as part of the design is also advisable. Orientations could be selected randomly, or the same orientation could be used for all cameras. Deviating slightly from the location and orientation selected by design (e.g., to attach the camera to a nearby tree or to avoid an obscured field of view) would not bias estimates provided field staff do not intentionally target habitat features known to be either preferred or avoided by the animals.

Empirical, design-based estimators of the encounter rate variance are robust to violation of the assumption that detections are independent events (Fewster et al. 2009, Buckland et al. 2015). However, in CT surveys we expect violations to be severe because we include multiple detections of the same animal during a single pass through the detection zone. We can avoid this assumption by estimating variances using a nonparametric bootstrap, resampling points with replacement (Buckland 1984, Buckland et al. 2001). Another consequence of lack of

105 independence is that the usual goodness-of-fit tests and model selection criteria are invalid
106 (Buckland et al. 2001). Methods for selecting among DS models when observations are not
107 independent are in development.

108 The assumption that detection is certain at zero distance could be violated by (1) animals
109 passing beneath the field of view (FOV) of the camera, (2) failure to identify the species because
110 only part of the animal is visible, and possibly (3) the delay between the time the sensor is
111 activated and the time the first image is recorded (the "trigger speed"), if animals directly in front
112 of the camera at a snapshot moment do not yield images. Such violations may be detectable
113 during exploratory analysis in the form of fewer than expected detections near the point, and bias
114 can be avoided via left-truncation (Buckland et al. 2001, Marques et al. 2007, e.g. Obbard et al.
115 2015). To minimize violations and ensure that detection probability is certain or high at some
116 distance near the point, cameras should be set at a height appropriate to the species of main
117 interest (Rovero and Zimmermann 2016). Lower heights would reduce the chance of small
118 animals passing beneath the camera at short distances, but would also reduce the range of
119 distances over which animals could be detected and therefore sample size and flexibility when
120 modelling the detection function. Pairs of CTs triggered by passive infrared (PIR) sensors and
121 mounted at the same location, height, and orientation, or one PIR CT deployed in combination
122 with other sampling devices (track plots, CTs triggered by pressure plates or active IR sensors)
123 could facilitate field tests of whether or not detection probability is close to 1 at short distances in
124 front of PIR CTs. Paired cameras mounted some distance apart targeting the same location
125 would not provide an effective test, but would provide the data needed to apply mark–recapture
126 distance sampling methods, which avoid this assumption (Buckland et al. 2004, Laake et al.
127 2011).

In traditional point transect surveys, human observers measure distances to each detected animal only once during each visit to a point, and effort at each point is the number of times it was visited. CTs remain at the point, but the snapshot approach discretizes the number of times we could potentially detect each animal (as T_k / t as described above). However, CTs detect only moving animals within the range of the sensor and the FOV of the camera, and can be programmed to record multiple still images, or video footage, each time the sensor is triggered (Rovero and Zimmermann 2016). These characteristics of CTs as observers must be taken into consideration. Observed distances upon first detection are expected to be positively biased because animals entering the detection zone through the arc of the sector would contribute a disproportionate number of observations at far distances. Bias would be slight if the time between snapshot moments (t) was small enough to ensure that the animals did not move far relative to the range of the sensor between snapshots, as then the observations would be representative of animals' continuous paths past the CTs. However, we prefer to avoid the potential for bias by assuming that the snapshot moments are selected independently of animal locations, and predetermining them as specific times of day to ensure that the assumption is met. Practical considerations constrain t. If t is large, animals that trigger the sensor might leave the detection zone before a snapshot moment arises, which would not cause bias but wastes data. As t is reduced, there would be fewer missed detections and larger samples as we record distance to each animal multiple times during a single pass in front of the CT. Eventually, improvements in the precision of $\widehat{D}$ with larger samples would become negligible because variation in the encounter rate among points would contribute most of the variation in estimated density. Reducing t further would then needlessly increase the time required to process and analyze the data. We suggest that values from 0.25 to 3 seconds are likely to be useful, with values at the

lower end of the range being more appropriate for faster-moving or rarer animals, and CTs with faster trigger speeds.

Programming cameras to record time-stamped video would make it straightforward to record distances at the predetermined snapshot moments. If still images are preferred, cameras should be programmed to record an image at the next several snapshot moments when triggered, or, if this is not feasible, to record a rapid series or "burst" of still images to ensure that images are recorded at times that align with snapshot moments. There should always be the potential for the camera to be triggered again immediately or after a minimal delay. Note that depending how cameras are programmed, the sample of distances observed in CT data may or may not comprise a realization from the detection function described by the probability that an animal at distance r triggers the sensor. If cameras record a single image at the subsequent snapshot moment, or a rapid series of images for $< t$ seconds, when the sensor is triggered, then each detection of an animal that triggers the sensor several times during a pass in front of a CT is a function of the sensitivity of the sensor. If cameras are set to record video, or a series of still images for $> 2t$ seconds, then all but the first detection is certain for as long as the animal remains in the FOV and the camera continues to record images. Furthermore, regardless of how the camera is programmed, any other animals in the FOV while the camera is recording images would contribute observations that do not depend on the sensitivity of the sensor. These differences do not invalidate the method provided we define the detection function as representing the proportion of locations at different distances which are recorded, regardless of whether an animal triggered the sensor at that distance.

Obviously, we can only estimate the density of populations that are available for detection by CTs. Similarly, because the sampling duration at each location (T_k) is part of the

model definition, we expect densities of animals that spend part of their time outside the vertical range of camera traps to be underestimated, and for the bias to be proportional to time animals are not available for detection. For example, with T_k set to the study duration, we expect $\widehat{D}$ of a species that spends all its time in the canopy to be zero, and of a species that spends half its time underground and the rest at ground level to be half of the true density. Negative bias would also result if animals went undetected only because movement was insufficient to trigger the sensor. To avoid this bias, either T_k should be defined as the amount of time that the entire population was available for detection while cameras were operating, or, equivalently, the proportion of time when animals were available for detection should be included as a parameter in the model. Animals are unavailable for detection when outside the vertical range of CTs, and may not be available when within this range depending on their level of activity. We explore this issue further in subsequent sections.

Simulations

We tested the method using simulations employing simple and complex models of animal movement and different sampling scenarios (see supplemental material). With the simple model, animals moved continuously at a constant speed and tended to maintain their heading. The complex model included variable speeds and tortuosities, and all animals rested for the same 12 hours of each day. We recorded the distance between cameras and animals within detection zones every two seconds, 24 hours per day. Where the complex model was used, we also collected data only when animals were moving, and reduced T_k by half accordingly when estimating density.

197 *Example: Maxwell's duikers in Taï National Park*

198 We used point transect DS methods to estimate the density of Maxwell's duikers within
199 the territory of the "east group" habituated chimpanzee community in Taï National Park, Côte
200 d'Ivoire (Després-Einspenner et al. accepted; Fig 1a). Maxwell's duikers were sampled from 28-
201 June through 21-Sept, 2014 at 23 camera traps (Bushnell Trophy Cam^{TM}; Model 119576C)
202 mounted at a height of 0.7 – 1.0 m and set to high sensitivity. Cameras were deployed with a
203 fixed orientation of 0˚ at the intersections of a grid with 1 km spacing and a random origin
204 superimposed over the study area (Fig. 1b). Realized sampling locations and orientations
205 deviated from the design by as much as 30 m, and 40˚, respectively, in order to mount cameras
206 on trees and to ensure there was some chance of detecting animals. During installation of each
207 camera, we measured horizontal radial distances from the camera, and recorded videos of
208 researchers holding distance markers, at 1 m intervals out to 15 m, in the center and along both
209 sides of the FOV. We estimated distances to filmed duikers by comparing their locations to
210 those of researchers in the reference videos. We set t = 2 seconds, and recorded the distance
211 interval within which the midpoint of each animal fell at 0, 2, 4, … , 58 seconds after the minute.
212 Larger distances were more difficult to measure precisely, so we assigned animals to 1-m
213 intervals out to 8 m, but binned observations between 8 and 10 m, 10 and 12 m, 12 and 15 m,
214 and beyond 15 m.

215 We excluded data from one camera because the FOV was largely obscured by vegetation,
216 and another which was placed on a slope and failed to detect any animals, but we included data
217 from a third camera that functioned normally but did not detect any duikers. Maxwell's duikers
218 sleep or rest for most of each night and for shorter periods during the day (Newing 1994, 2001).
219 We assumed they would not be available for detection overnight and excluded the hours of

darkness (19:00 – 6:00) from T_k *a-priori*. We accounted for limited availability during the daytime three different ways. First we naively assumed that all duikers were active by 6:30:00 and remained so through 17:59:59, included distances observed during this interval in a "daytime" data set, and defined temporal effort at each location (T_k / t) as the number of 2-second time steps during that time interval (20699), multiplied by the number of sampling days. Second, we assumed that all animals were available only during apparent times of peak activity (6:30:00 – 8:59:59 and 16:00:00 – 17:59:59) and recalculated temporal effort and censored distance observations accordingly (T_k / t per day = 8098). Third, we defined T_k and included observations as above for the daytime data set, and included an independent estimate of the proportion of time captive Maxwell's duikers were active during the same time interval (0.64; Newing et al. 2001) in the denominator of Eq. 2. We included only data from complete days when cameras were operating and not visited by researchers.

We fit point transect models in program Distance (version 7.0; Thomas et al. 2010), defining survey effort at each location as $\frac{\theta T_k}{2\pi t}$. The cameras had an AOV of 42˚, and a wider effective angle of the sensor (Trailcampro.com 2015), so we set θ = 42˚ or 0.733 radians. We considered models of the detection function with the half-normal key function with 0, 1 or 2 Hermite polynomial adjustment terms, the hazard rate key function with 0, 1, or 2 cosine adjustments , and the uniform key function with 1 or 2 cosine adjustments. Adjustment terms were constrained, where necessary, to ensure the detection function was monotonically decreasing. We selected among candidate models of the detection function by comparing AIC values, acknowledging the potential for overfitting because many observations were not independent. We present measures of uncertainty derived from design-based variances ("P2" of

242 Fewster et al. 2009, Web Appendix B), and from 999 bootstrap resamples, with replacement,
243 across camera locations.
244
245 **Results**
246 *Simulations*
247 Where we used the simple model of animal movement, and where we used the complex
248 model of animal movement and collected data only when animals were active, $\hat{D}$ was unbiased
249 (Table S1). Results were biased and erratic when we recorded distances to resting animals (see
250 supplemental material for details). Design-based variances were smaller than the sampling
251 variance of $\widehat{D}$ across iterations, and associated confidence interval coverage was <90% (Table
252 S1). Where we estimated variance by bootstrapping, the coefficient of variation was 0.119,
253 similar to the sampling variance of $\widehat{D}$, and CI coverage was 93.6% across 1000 iterations.
254 Doubling spatial sampling effort improved precision, slightly more so where we doubled the
255 number of locations as opposed to θ (Table S1).
256
257 *Example: Maxwell's duikers in Taï National Park*
258 We obtained 11324 observations of the distance between Maxwell's duikers and cameras
259 in 806 different videos. Duikers were rarely filmed during hours of darkness. The frequency of
260 detection increased steadily after 6:00 to a maximum between 6:30 and 7:00 and remained
261 relatively high until 9:30, after which it decreased slightly and remained relatively low until
262 16:30, then increased again and remained high until 18:00, then declined gradually until 19:00
263 (Fig. 2). Duikers were always active when detected; CTs did not record any duikers that were

asleep or stationary for an entire minute. We recorded 11180 distances from 6:30:00 through 17:59:59, and 6274 during times of peak activity.

Exploratory analyses revealed no evidence of data collection errors, and a paucity of observations between 1 and 2 m but not between 2 and 3 m, so we left-truncated at 2 m. Fitted detection functions and probability density functions were heavy-tailed when distances > 15 m were included, so we right-truncated at 15 m. Truncating removed 8% of observations from the daytime data set, leaving n = 10284, and 6.5% of observations from the peak activity data set, leaving n = 5865. Mean encounter rates (mean numbers of duikers observed per 2-second time interval) across all points were 3.27×10^{-4} during the daytime and 4.76×10^{-4} during times of peak activity. Encounter rates were highly variable among locations but did not exhibit an obvious spatial pattern across the study area, and there was no evidence of spatial autocorrelation (Moran's I P = 0.47; Fig. 3).

When we fit the hazard rate model with two adjustment terms to the daytime data set, the detection function was not monotonically decreasing, so this model was not considered for estimation. All models were fitted successfully to the peak activity data set. The hazard rate model with no adjustments minimized AIC and was used to estimate density in both cases. Probability density functions of observed distances and relationships between detection probability and distance were similar (Fig. 4). Detection probability was ~1.0 within 5 m and 0.05 at 15 m; effective detection radii were 9.1 and 9.4 m from the daytime and peak activity data sets, respectively.

We expected to underestimate density where we assumed duikers were active all day; $\widehat{D}$ was 37% higher when we included only data from times of peak activity (Table 1). Including an independent estimate of the proportion of time active during the daytime as a parameter in the

model fit to the daytime data set yielded a still higher estimate ("Active daytime" in Table 1). Measures of uncertainty in the proportion of time active were not available (Newing et al. 2001) so did not contribute to the variance of $\widehat{D}$. Bootstrap variances were larger than design-based analytic variances (Table 1). The vast majority (99.8%) of the design-based variance of $\widehat{D}$ was attributable to the variation in encounter rate between locations, and only 0.2% to detection probability.

Discussion

Simulations demonstrated the potential for the method to yield unbiased density estimates, but also that animals' activity patterns must be accounted for. Where simulated animals rested for half of each day and we set T_k equal to the survey duration, the most common scenario was that animals did not rest in front of CTs and negative bias in $\widehat{D}$ was proportional to the time spent resting. When we recorded distance at each snapshot moment while animals rested in front of CTs, the encounter rate and therefore $\widehat{D}$ was higher on average, but the shape of the detection function was strongly affected, leading to erratic estimates and cases where models could not be fitted to the data. In practice, it is unlikely that we would detect animals while they sleep or rest because movement will be insufficient to trigger the sensor. Therefore, estimates of the proportion of time animals are active within the vertical range of CTs will be required to avoid negatively biased $\widehat{D}$. Ideally, this proportion would be estimated from data collected concurrently with the distance data to ensure it is representative. Fortunately, the temporal distribution of camera trap detections is informative regarding animal activity patterns (Lynam et al. 2013, Cruz et al. 2014, Rowcliffe et al. 2014). If it is reasonable to assume that the entire population is available for detection for any part of each day, additional data would not be

required to estimate $\widehat{D}$ accurately, because we could either (1) analyze only the data collected at that time, censoring effort and distance data from other times, or (2) estimate the overall proportion of time active directly from the CT data (e.g. Rowcliffe et al. 2014). Newing's (1994) data from Taï indicated that there was no time at which all wild duikers could be assumed to be active. If this was true during our survey, we may have underestimated density where we did not correct for limited availability within the time included in T_k, because even at times of peak activity some animals may have been resting and unavailable for detection. Activity data from wild duikers were presented only as figures and could not be converted into estimates of the overall proportion of time active (Newing 1994). We therefore relied on the assumption that activity data from captive duikers (Newing 1994, Newing et al. 2001) were representative of activity patterns during our survey. If this assumption held, then the density estimate calculated using their estimate of the proportion of time active during the day should not be biased as a result of limited availability. We suggest that the need to account for availability should not pose a serious obstacle to reliable estimation of the density of many species, but for others, notably ectotherms, and semi-arboreal and fossorial species, it will require careful consideration, and possibly additional data. We further suggest that combining Rowcliffe et al.'s (2014) or similar methods for estimating the proportion of time active from detection times at CTs with the point transect method described here could yield accurate density estimates for many species from CT data alone.

Avoidance of, or attraction to, CTs would bias encounter rates and therefore density estimates. Some species exhibit complex responses to CTs or are particularly wary of humans (Séquin et al. 2003). If behavioural responses are expected or apparent in images of detected animals, CTs could be deployed prior to the start of the actual survey to allow animals to become

accustomed to them and for signs of human presence to dissipate. Similarly, effort and distance data from times when animals may have been displaced from the trap sites by humans visiting them to download data, replace batteries, etc., should be censored.

The probability of detection at PIR CTs is lower at greater angles from the center of the FOV, due to a combination of the trigger speed, the effective horizontal angle of the sensor relative to the AOV of the camera (which varies among CT models) and possibly reduced sensitivity of the sensor at the periphery of its horizontal range (Rowcliffe et al. 2011, Rovero et al. 2013, Rovero and Zimmermann 2016). This introduces heterogeneity in the detection function. Fortunately, provided that detection is certain at zero distance, the pooling robustness property ensures that estimation is unbiased in the presence of heterogeneity in detectability among individuals (Buckland et al. 2004), and this also applies to heterogeneity caused by differences in angle at different snapshot moments. However, if detection probability at high θ is much lower than in the centre, fitted models of the detection function might show a rapid drop in detection probability near the point, whereas detection functions with a gradual decrease near the point are preferred for stable density estimation (Buckland et al. 2001). The expected distribution of angles within a sector within which the sensor is fully effective is uniform. We recommend that researchers measure angles as well as distances to detected animals (e.g. Carravaggi et al. 2016), and test for departures from the uniformity assumption at increasing angles as part of their exploratory analysis. If departures are apparent, the data could be truncated to exclude observations beyond an angle within which the distribution is approximately uniform, in which case θ should be set to two times the truncation angle rather than the AOV of the camera in the definition of effort. An alternative approach that would allow us to retain all of the data would be to develop a two dimensional detection function where detection probability

depends on both radial distance and angle from center, using methods similar to those developed by Marques et al. (2010). We expect heterogeneity with angle to be more severe with CT models with narrow horizontal ranges of the sensor relative to the AOV of the camera, or slow trigger speeds, and where faster-moving animals are sampled. CTs with fast trigger speeds, short recovery times, and curved array Fresnel lenses (which provide a wide effective angle of detection such that the camera begins recording images as or even before the animal enters the FOV; Rovero and Zimmermann 2016) could reduce or eliminate differences in detection probability at different angles in future studies.

The encounter rate variance accounted for the vast majority of the design-based variance in duiker density, and variances around $\widehat{D}$ were larger than for simulated data despite similar sample sizes. Real populations exhibit clumped or patchy distributions and non-random movement, leading to variable encounter rates among sampling locations and hence greater uncertainty in $\widehat{D}$ (Buckland et al 2001, Fewster et al. 2009); the small area sampled at each location exacerbates this problem. Increasing the area sampled will therefore enhance precision, more so than would increasing temporal effort at a point. Theory predicts that increasing the number of points will yield the largest improvements to precision (Buckland 1984, Fewster et al. 2009). That the improvement in precision in simulations was only slightly greater where we doubled the number of sampling locations than where we doubled θ is not representative of real studies because the expected spatial distribution of animal locations was uniform, and movement was random. Coefficients of variation around $\widehat{D}$ for duikers were >35% despite large samples of distance observations, so we recommend that future studies employ more points to improve precision.

The density of Maxwell's duikers at Taï was recently estimated as 1.6 / km^2 from line transect DS surveys (N'Goran 2006). However, line transect sampling by human observers is believed to severely underestimate densities of forest-dwelling animals in general, and forest antelopes in particular, due to effects of evasive movement and behaviour in response to observers on both the encounter rate and the distribution of observed distances (Koster and Hart 1988, Jathanna et al. 2003, Rovero and Marshall 2004, 2009, N'Goran 2006, Marshall et al. 2008, Marini et al. 2009). Estimates of sign density from line transect surveys are frequently converted to estimates of animal density, but this is expected to yield biased estimates in the absence of local and concurrent estimates of sign production and decay rates, which are time-consuming to estimate (Plumptre 2000, Kuehl et al. 2007, Todd et al. 2008). Dung surveys may further require genetic analysis to identify the species (Bowkett et al. 2009). Distance sampling with CTs apparently avoided the underestimation characteristic of line transect surveys of live animals, in less time than would be required to obtain reliable estimates from sign surveys.

The recent proliferation of CT studies is providing new information about wildlife in diverse habitats (Burton et al. 2015, Rovero and Zimmermann 2016). Where estimating the density of a rare but individually identifiable species is the primary research objective, it may be preferable to deploy CTs non-randomly in order to obtain sufficient detections of individuals to estimate density by SECR (Wearn et al. 2013, Cusack et al. 2015*b*, Després-Einspenner et al. accepted). However, multiple research objectives can be addressed, and useful data for multiple species obtained, if CTs are deployed according to a randomized design (MacKenzie and Royle 2005, Wearn et al. 2013, Burton et al. 2015, Dénes et al. 2015). The size of unmarked populations can then be estimated from CT data using Poisson and negative binomial GLMs or hierarchical N-mixture models (Dénes et al. 2015), but population density is of greater interest

401 because it is more biologically relevant and comparable across studies. Densities of unmarked
402 animal populations can only be estimated from CT data using SECR models for unmarked
403 populations, the REM, or DS methods; the latter two require randomized designs (Rowcliffe et
404 al. 2008, Buckland et al. 2001). SECR methods for unmarked populations require intensive
405 designs, and even then estimates will often be too imprecise to be useful unless a subset of the
406 population can be reliably identified (Chandler and Royle 2013, Saout et al. 2014). The REM
407 requires an estimate of the average speed of animal movement, assumes that detection is certain
408 within an estimable area in front of the camera, and makes use of only one observation from each
409 detected animal (Rowcliffe et al. 2008). Our point transect approach requires an estimate of the
410 proportion of time animals are available for detection, assumes that detection is certain only at
411 zero distance, and multiple observations from each detected animal inform detection probability
412 estimates. We expect the extension of point transect DS methods to provide an effective and
413 efficient tool for estimating animal density and to enhance the information derived from CT
414 surveys.
415

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422

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Table 1. Densities of Maxwell's duikers in Taï National Park, 2014, estimated using different methods to account for limited availability for detection. Bootstrap confidence intervals were calculated using the percentile method.

		Design-based		Bootstrap	
Availability	$\hat{D}$	CV	95% CI	CV	95% CI
Daytime	10.6	0.27	6.1–18.3	0.40	5.0–21.8
Peak activity	14.5	0.30	7.8–26.9	0.36	6.1–26.9
Active daytime	16.5	0.27	9.5–28.6	0.40	7.7–34.1

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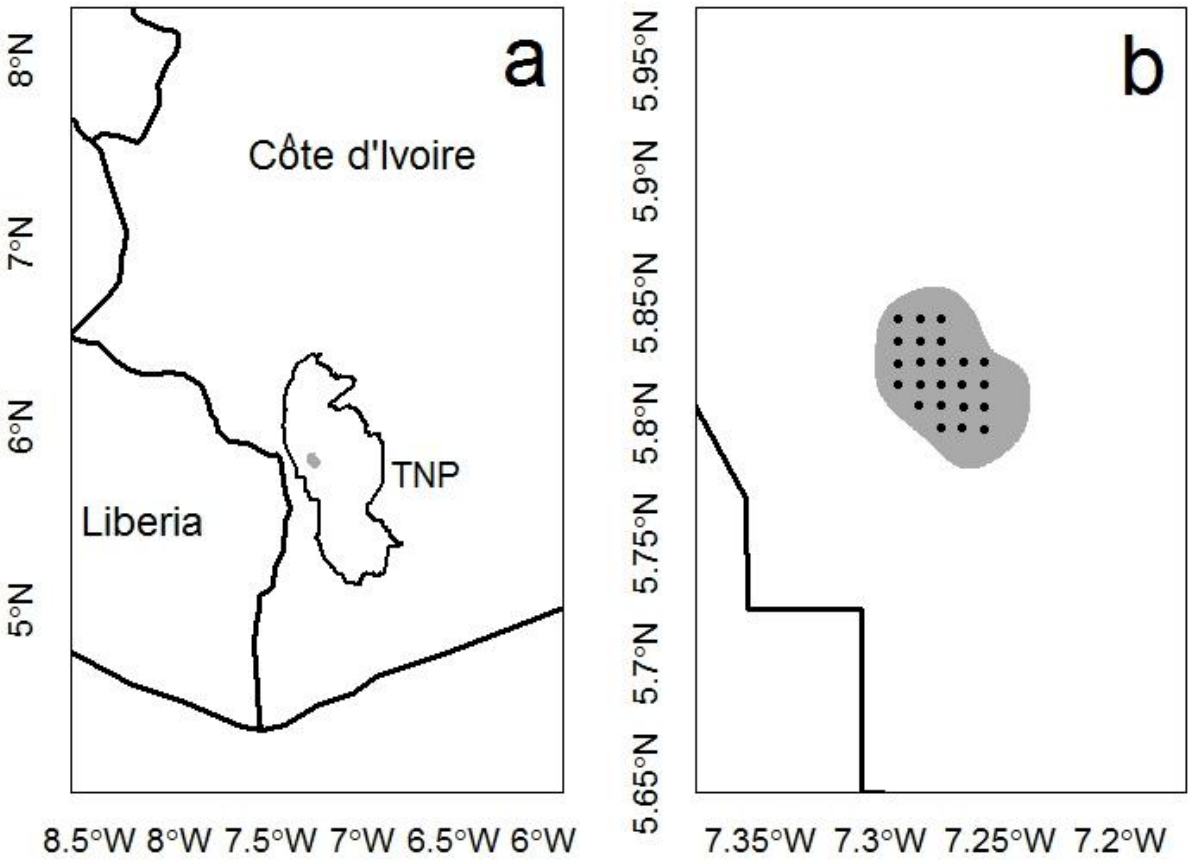

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600 Figure 1. Location of the study area (grey polygon) in Taï National Park (TNP), Côte d'Ivoire,
601 2014 (a), and (b) locations of 23 camera traps deployed in a grid with 1 km spacing within the
602 study area.

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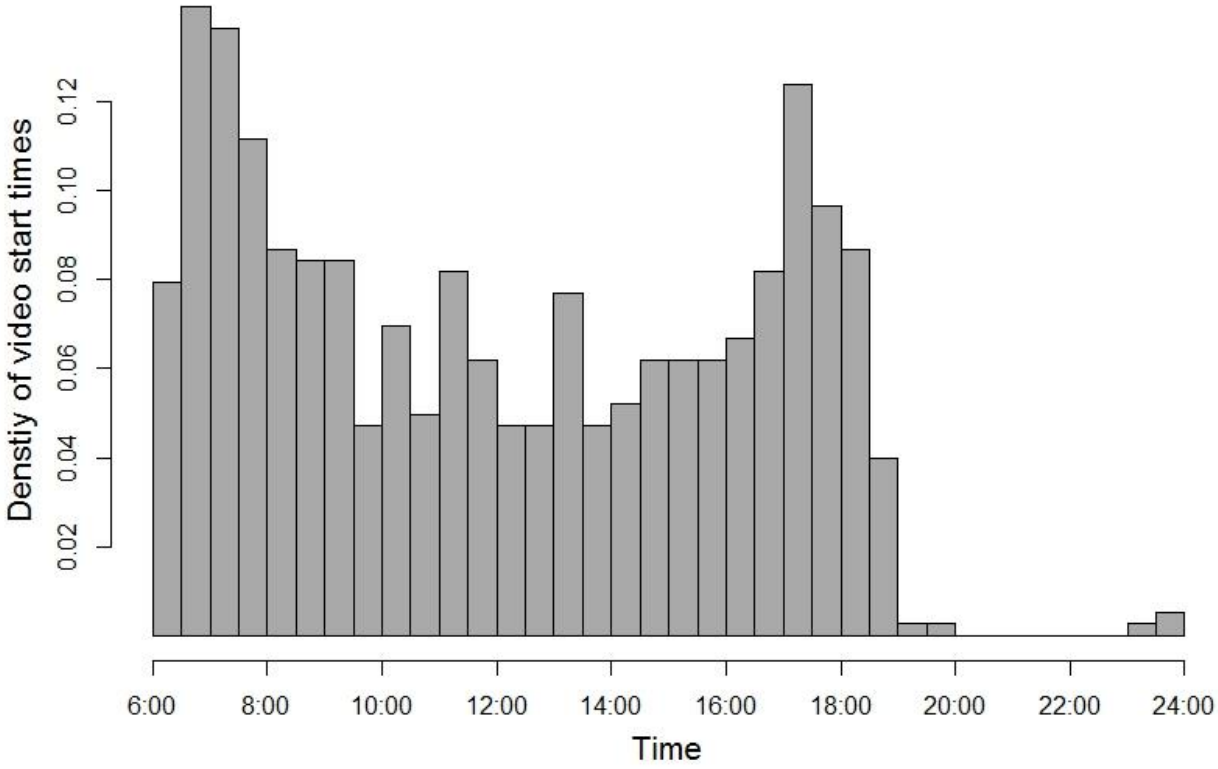

611 Figure 2. Histogram of start times of videos of Maxwell's duikers in Taï National Park, Côte

612 d'Ivoire, 2014.

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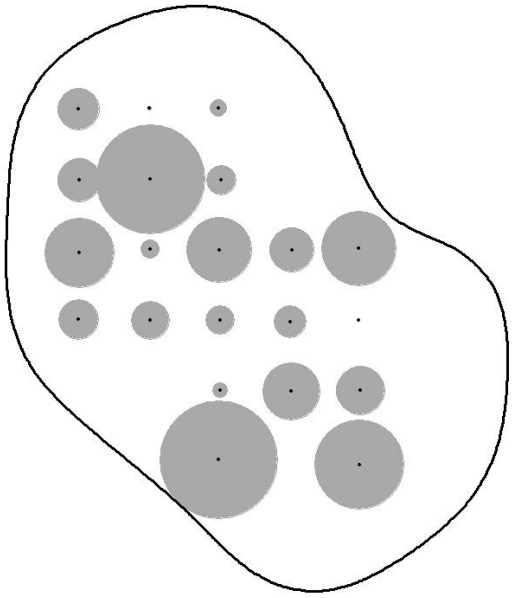

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616 Figure 3. Variation in encounter rates of Maxwell's duikers among 21 camera trap locations in
617 Taï National Park, Côte d'Ivoire, 2014 (range 0.00 – 1.45 × 10^{-3}). The areas of the grey circles
618 are proportional to the encounter rates.

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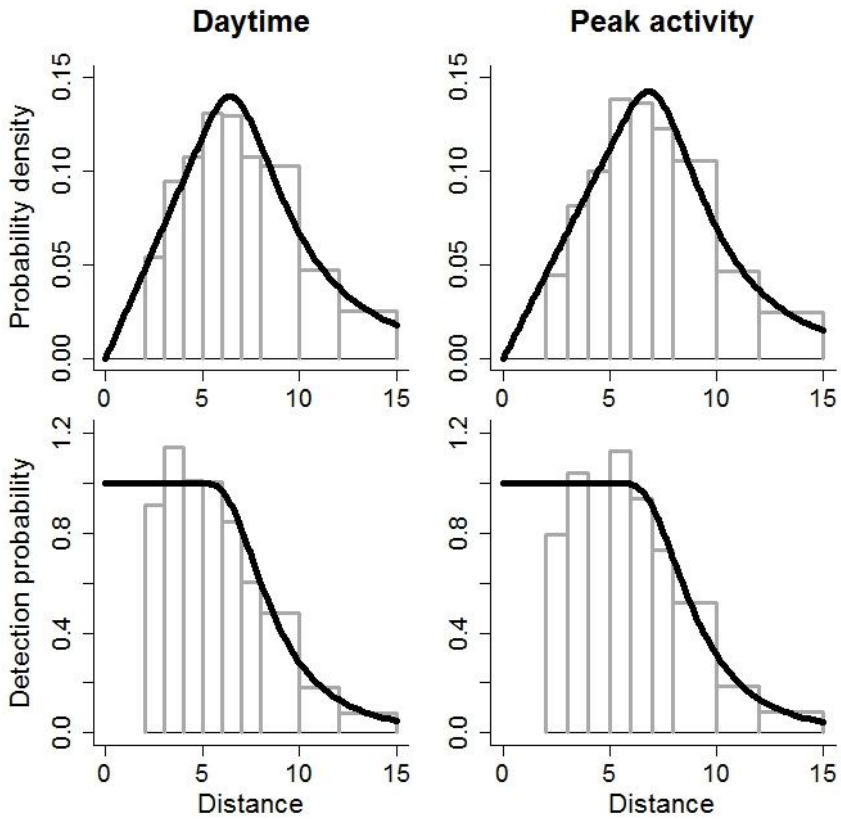

621 Figure 4. Probability density functions of observed distances (top) and detection probability as a
622 function of distance (bottom) from hazard-rate point transect models fit to data from Maxwell's
623 duikers in Taï National Park, 2014, collected during the daytime (left) and during times of peak
624 activity (right).