A practical guide for estimating animal density using camera traps: Focus on the REST model

HONGO, Shun

The Center for African Area Studies, Kyoto University

hongo.shun.8s@kyoto-u.ac.jp

NAKASHIMA, Yoshihiro

College of Bioresource Sciences, Nihon University

yosshi1215jp@yahoo.co.jp

YAJIMA, Gota

College of Bioresource Sciences, Nihon University

wildlife.hunter0712@gmail.com

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Person to whom correspondence:

Hongo, Shun

46, Yoshida Shimoadachi-cho, Sakyo-ku, Kyoto, 606 8501, Japan

Phone: +81 75 753 7359

Email: hongo.shun.8s@kyoto-u.ac.jp

Abstract

Estimating animal density and finding the factors that influence it are central in wildlife conservation and management but challenging to achieve, particularly in forested areas. Camera trapping is a pervasive method in forest mammal survey and a plausible technique to overcome this challenge. This report provides a practical guide for conducting a camera trap survey to estimate the density of forest mammals applying the random encounter and staying time (REST) model. We firstly provide a brief explanation about the structure and assumptions of the REST model. Next, we describe essential points during different steps in planning a survey: determination of objectives, design of camera placement, choice of camera models, camera setting, the layout of the camera station, and list of covariates. We then develop detail-oriented instruction for conducting a survey and analysing the obtained video data. We encourage camera trap surveyors to provide the practised protocols of their surveys, which will be helpful to other camera trappers.

Keywords

Camera placement design; camera station layout; forest mammals; survey plan; trail camera; video analysis; wildlife monitoring

Introduction

How can we accurately estimate the population density of wild animals? How can we reliably assess the factors influencing their density? These two questions are of common importance to field ecologists, conservationists and wildlife managers working with animal taxa (Elliot & Gopalaswamy 2017; Burgar et al. 2018; Santini et al. 2018; Cavada et al. 2019). Forested areas, which host many biodiversity hotspots (Myers et al. 2000; Marchese 2015; Hu et al. 2021), are particularly challenging to effectively address the above issues due to poor accessibility and visibility compared to open landscapes such as woodlands and grasslands (Kamgaing et al. 2018).

Camera traps—motion-triggered automatic cameras with (often passive infrared) sensors (Apps & McNutt 2018b)—have been introduced into forest animal surveys as a powerful tool to solve this conundrum (O'Connell et al. 2011; Burton et al. 2015). Although the camera trap survey requires a relatively high initial investment, it has a major advantage in labour costs: No one has to work in the survey area except for the installation, regular operation checks and retrieval. And camera trapping is less invasive for both vegetation and animals than most conventional methods. For example, there's no need to cut many transects in the forest or observe animals directly, as is required in the line-transect distance sampling (Buckland et al. 2001; Buckland et al. 2015). Hence, camera trapping has become a standard method for forest mammal surveys (McCallum 2013).

With a sufficient number of camera traps, surveyors may already be sitting on a gold mine of "reliable density estimates"—but they still have to dig. In this case, they don't need a pickax or shovel but a dedicated statistical model and a survey plan tailored to the model. Many models are available for animal density estimation (Iijima

2020). Some are applicable for “marked”, i.e., individually identifiable, populations; others can be used for “unmarked” populations. And some can be implemented using camera traps (Gilbert et al. 2021), others not. Among them, the random encounter and staying time (REST) model (Nakashima et al. 2018) estimates the density of unmarked population from camera trap data alone. We believe that, together with several alternatives (Chandler & Royle 2013; Howe et al. 2017), the REST model is one of the most promising methods for this purpose.

As with any models, the REST model has several assumptions to ensure unbiased, accurate density estimation. Surveyors need to carefully plan the survey to meet them. Surveyors can refer to previous studies applying the REST model (Garland et al. 2020; Yokoyama et al. 2020), but research papers usually describe the survey method details only briefly. This makes it difficult for them to prepare plans with confidence. A more practical guide for the density estimation survey is necessary to avoid falling into unexpected pitfalls. Here, we provide detailed instruction for conducting density estimation surveys of forest animals using camera traps and the REST models. We develop detail-oriented discussions of the complications that need to be taken into account when actually conducting the survey. After briefly introducing the theory, structure and assumptions of the REST model, we discuss various aspects to be kept in mind when preparing for and conducting the survey and analysing the camera-trap data.

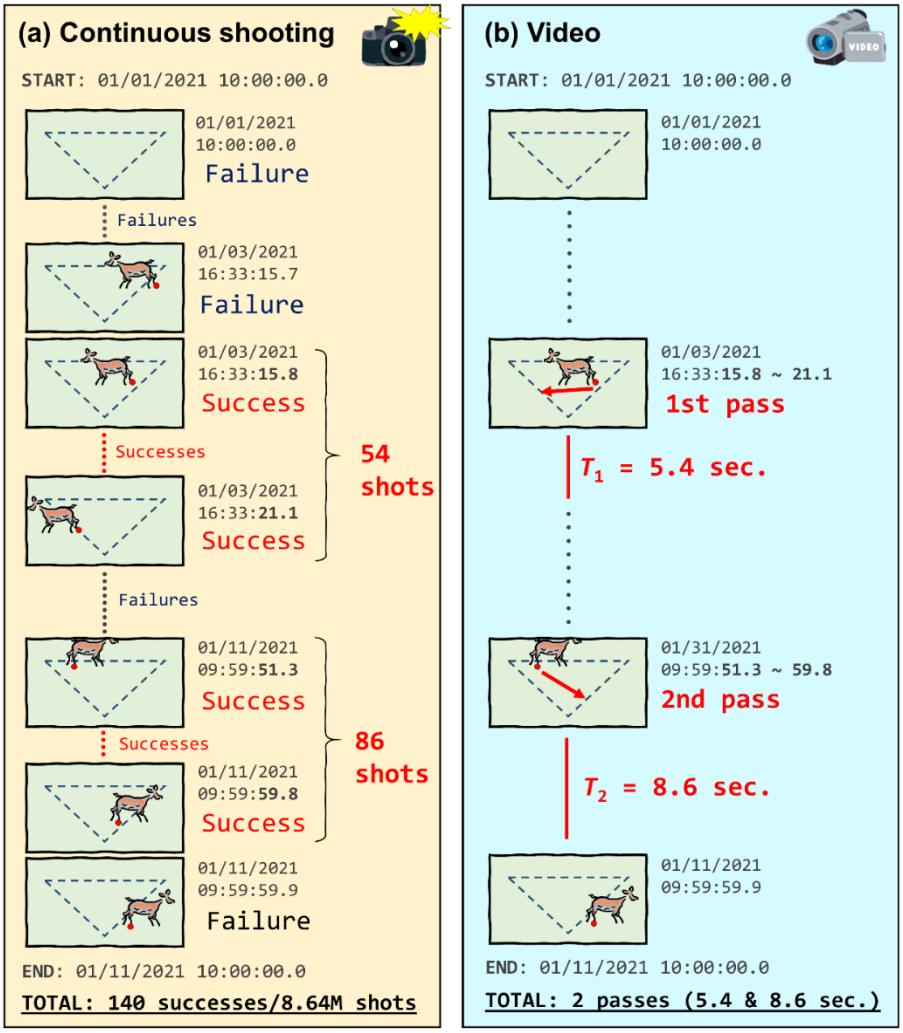
REST model: a brief explanation

The REST model was devised following the ideas of the random encounter model (REM) (Rowcliffe et al. 2008). It formulated the number of animal passes as a function

of the animal density, “detection zone” (the area that cameras can capture all animals passing through), survey period and travel speed. The REM, however, requires measuring the animal travel speed independently to camera trapping, which makes the model difficult to implement in wildlife surveys. The REST model has overcome this problem by focusing on “staying time”—the inverse of travel speed—in the detection zone (Nakashima et al. 2018). To understand it, let’s consider how we can express the expected value of the total staying time of animals passing through a camera’s detection zone. For the sake of simplicity, we consider here a solitary mammal species, although Nakashima et al. (2018) showed that the REST model could also be applied to pair-living mammals.

There are two approaches (Fig. 1). The first one thinks that only one camera trap is placed and operates in the “continuous shooting mode” (Fig. 1a). It takes a series of pictures at very short intervals (say 0.1 s) for the entire survey period (from installation to retrieval of this camera). If we knew the animal density (D), the expected success rate of photographing the animal would be expressed as Ds, where s is the area of the detection zone. If the survey period (H) is sufficiently long, then the expected total staying time would be DsH.

The second approach assumes that many camera traps work in the “video mode” to take videos throughout when an animal is in the detection zone (Fig. 1b). From the videos, we can count each camera’s number of times that animals passed through the detection zone (Y). And we can measure the staying time of each pass (T). We can, therefore, simply represent the total staying time in a camera as a product of their expected values, $\mathrm{E}(Y) \cdot \mathrm{E}(T)$.



- Animal density = D (km^{-2})
- Detection zone per camera = s (km^2)
- Expect. num. of indiv. per shot = Ds
- Survey period = H (sec.)

- Expect. num. of passes = E(Y)
- Expect. staying time) = E(T) (sec.)

Total staying time per camera: $\boldsymbol{DsH = E(Y) \cdot \mathrm{E}(T)}$

Fig. 1. Pattern diagrams of two parallel cases—(a) continuous shooting mode and (b) video mode—for estimating the total staying time of animals passed through a camera trap's detection zone. In both cases, solitary animals passed twice through the detection zone of s km^2 during a survey period (H) of 10 days (= 864,000 s). A red circle on the right hind toe indicates the focal point for determining the entry of animals in the detection zone and measure their staying time.

Having expressed the total staying time in two different ways, we now have the following equation:

$$DsH = \mathrm{E}(Y) \cdot \mathrm{E}(T) \tag{1}$$

Thus,

$$D = (\mathrm{E}(Y)\,/\mathrm{H}) \cdot (\mathrm{E}(T)/s) \tag{2}$$

Equation 2 formulates the animal density as a product of the expected detection rate and the expected staying time in a detection zone. One can predetermine *s* and *H* but have to estimate E(*Y*) and E(*T*) from the data. To do so, Nakashima et al. (2018) proposed a negative-binomial distribution to model the number of passes; they used exponential, gamma, log-normal and Weibull distributions for staying time. As in generalised linear models (GLMs), we can estimate the distribution parameters using the maximum likelihood estimators (for frequentists) or as the posterior probability distributions (for Bayesians). Nakashima et al. (2018) also described how to deal with the right-censored staying time, where leaves from the detection zone were not observed due to the camera's time interval setting.

Incorporate habitat covariates

As we saw above, animal density can be expressed as a mixture of two GLMs. So it's now possible to model differences in density due to various environmental and anthropogenic effects. Nakashima et al. (2020) expanded the basic REST model to incorporate the habitat covariates—such as altitude, slopeness, distance from human settlements—into the model as the linear predictors of the expected staying time and the

density. When φ and D represent the expected staying time and density, respectively, we can consider that they are specific to camera stations with the following form:

$$\log(\varphi_i) = \alpha_0 + \sum_{k=1}^{K} x_{ik}\alpha_k \tag{3}$$

$$\log(D_i) = \beta_0 + \sum_{k=1}^{K} x_{ik}\beta_k \tag{4}$$

where x_{ik} is the kth habitat covariates at camera station i. We can also include random effects in the linear predictors to explain, for example, station-specific random differences in staying time. The relationship between these parameters and the expected number of detections at station i, θ_i, with the form below:

$$\log(\theta_i) = \log(D_i) - \log(\varphi_i) + \log(s) + \log(H_i) \tag{5}$$

Nakashima et al. (2020) proposed that habitat covariates and random effects affect rate parameter for exponential and gamma distributions, mean log parameter for log-normal distribution, and scale parameter for Weibull distribution.

Constructing a model for each of the different hypotheses, analysts have many models with different combinations of covariates. If they intend to compare the models in terms of better prediction of animal density, analysts can use information criteria, such as Akaike Information Criterion (AIC; Akaike 1973, 1974) or Watanabe–Akaike Information Criterion (WAIC; Watanabe 2010). If you intend, by contrast, to examine the presence of habitat effects, they may choose an appropriate statistical test.

Assumptions and limitations

Every model has its own assumptions and limitations, and the REST model is no exception. The REST model has four major assumptions (Nakashima et al. 2018) (Table 1). Surveyors have to carefully plan the survey to meet them.

Table 1 Assumptions of the random encounter and staying time (REST) model.

Assumption	Description	Insights
I. Closed population	The population density must not vary over the survey period.	The survey period should be sufficiently short that the density does not change significantly.
II. Random sampling	Camera traps must be placed randomly with respect to the animal's spatial distribution.	Surveyors must not arbitrarily select animal trails or mineral licks as camera stations.
III. Animal unresponsiveness	Cameras or camera stations must not change animal movement and behaviour.	Use of lure and baits must be avoided, and vegetation clearing around cameras must be minimised.
IV. Perfect detection	Camera traps must detect all animals that entered the detection zone, and analysts must correctly identify the species from images.	The detection zone has to be carefully determined after rigorous tests.

A further practical limitation is that cameras can hardly observe the animal staying time during the long rest. In a simple example, a strictly diurnal species is rarely detected at night unless we place millions of cameras. There are two choices here: purchase and installation of millions of cameras to obtain sufficient data of staying time during the night rest; or post hoc exclusion of night time—when detectable animals are "absent"—from the survey period. Realists would take the latter, and we recommend it. Rowcliffe et al. (2014) developed a method to estimate the proportion of time that animals are on the move (referred to as "activity level") with time-of-detection data from camera traps. Multiplying the survey period by the activity level can correct the survey period to represent only when the animals are moving. Accordingly, we can rewrite equations 2 and 5 as follows:

$$D = \mathrm{E}(Y) \cdot \mathrm{E}(T)/(sH \cdot p) \tag{6}$$

$$\log(\theta_i) = \log(D_i) - \log(\varphi_i) + \log(s) + \log(H_i) + \log(p) \tag{7}$$

where p is the activity level of the focal population. Nevertheless, this method assumes that all animals in the population are active at the peak of the activity cycle (Rowcliffe et al. 2014). Species whose activity rhythm doesn't synchronise between individuals, including many cathemeral mammals, do not meet this assumption, and so their density will be underestimated.

Planning a survey

Set objectives

Field surveys need firm objectives to be carried out. The following two points need

mature consideration. First, the two different objectives are often confounded: (i) estimating the mean population density and (ii) examining the effects of covariates on the density. In implementing the REST model, we can categorise these two objectives in terms of the absence (Nakashima et al. 2018) or inclusion (Nakashima et al. 2020) of explanatory variables in the linear predictors for the staying time and density. When surveyors aim to estimate the mean density, the coordinates of camera-trap stations should ideally be generated at random in the study area, without regard to the distance between the stations. There's also principally no need to quantify habitat conditions. On the other hand, if surveyors want to find some factors explaining the variation in animal density, they have to carefully plan the camera placement design so that each candidate explanatory variable has sufficient variation. Factors of interest can vary widely, so they may place cameras from the foot to the top of the mountain, from the vicinity of villages to remote forests, or in both logging and protected zones. Moreover, sampling from each camera should be independent, so they have to set the distance between the stations larger than the radius of the home range of focal animal species.

Second, a good survey objective must explicitly define the scope of the inference: The plan has to clearly explain your choices regarding the focal species, the survey area and the survey period. Moreover, these choices should be justified in terms of both convincingness and feasibility. Suppose a surveyor has set up a survey area of 100 km^2 in the south part of a 1000-km^2 national park and discussed the mean density of the whole park from the results. This would hardly convincing because the survey area is not necessarily representative of the entire park. She has two ways to solve this problem: Extend the survey for the whole park, or, if this isn't feasible, change the survey objectives. Also, surveys should usually be carried out in the dry season, when

the risk of camera failure due to rain or humidity is low. But if the focal species are known to exhibit seasonal migratory behaviour, rainy-season surveys may also be necessary to make convincing conclusions.

Decide on the camera placement design

Once you set suitable objectives, focal species and areas and periods of the survey, decide how positioning the cameras. To do so, we can easily generate numerous points on a computer-displayed map using free geographic information system (GIS) software such as QGIS (QGIS Development Team 2021). Because of its easiness, however, we are sometimes lost in the face of a massive number of options. To help surveyors out of this quandary, we introduce some suitable camera placement designs and some to be avoided.

Suitable designs

Random placement (Fig. 2a) is the first choice when estimating the mean density. It's easy to draw—all we have to do is select the survey area and let the computer generate random points for a number of camera stations. This placement is the most reliable in ensuring random and unbiased sampling from the survey area. In a large survey area, however, this placement may be impractical as the deployment is too labour-intensive and time-consuming. Moreover, if you aim to identify covariates relating to the density, this placement may cause problems because randomly placed cameras cannot specify the range of target explanatory variables.

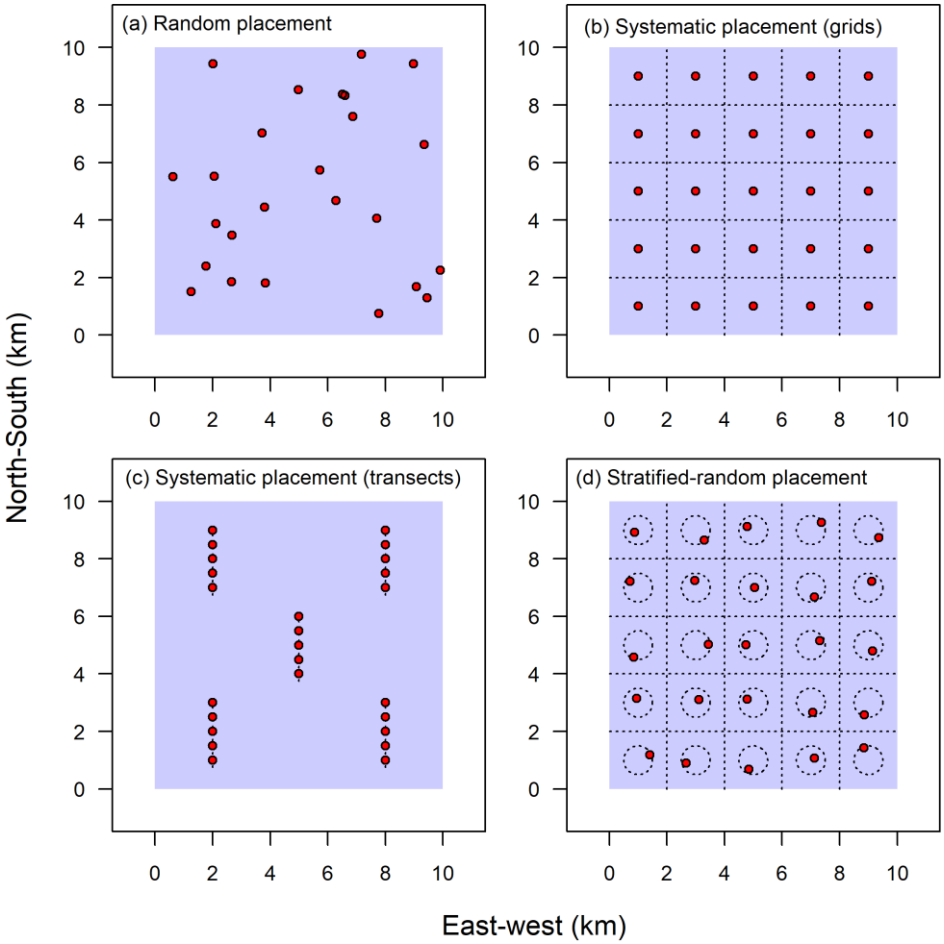


Fig. 2 Schematic maps of four suitable camera placement designs: (a) random placement, (b) systematic grid placement, (c) systematic transect placement, and (d) stratified-random placement. In each panel, 25 points for camera trap stations (red circles) are generated in a 100-km^2 survey area (blue square).

Systematic placement is an elegant way to find factors explaining variations in the density. When this placement is adopted, surveyors typically set up a square grid over the survey area, setting camera stations at each grids' centre. In this "grid design" (Fig. 2b), camera station points are evenly spaced throughout the survey area. To ensure data independence, the length of the grids' sides should be greater than the radius of the subject animals' home range. It may be possible to estimate the mean

density using the grid placement, but there is a risk of bias in the estimated density and confidence intervals. In a survey area where logging roads or other structures are built at nearly equal intervals, for example, equally-spaced cameras may bias the estimates because particular environmental areas are sampled disproportionately.

Alternatively, surveyors may set line transects evenly over the survey area and then set camera stations at regular intervals along the transects. This “transect design” (Fig. 2c) is more effortless when installing and managing cameras than the grid design. This design needs, however, hierarchical modelling in statistical analysis because stations are nested within and between transects. One step further, this design allows comparisons of density between different zones in a survey area by deliberately placing transects in each zone. It should be noted, however, that the transect method does not provide an accurate estimation of the mean density for the whole area.

Random placement is too labour-intensive; systematic designs risk biased sampling. A good compromise to solve this dilemma is *stratified-random placement* (Fig. 2d). This is a mixture of the above two placements: Like a systematic placement, set up a coarse square grid but generate a random point per grid for camera stations. If one wishes to avoid cameras coming too close to each other, draw a circle of an appropriate size in each grid’s centre and generate a random point within it. Cameras will not be placed out of the circles, so data independence is guaranteed. By carefully planning this placement, the two objectives (mean density estimation and examination of covariates) may be set simultaneously. Furthermore, this placement has many possible variations. For example, stratify the survey area according to vegetation types on a GIS map and then generate random station points so that the number of points is proportional to the area covered by each vegetation type. In this way, one can estimate the mean density of the entire area with a small bias and test the differences in density

between vegetation types.

Methods to be avoided

Targeted placement should be avoided when working for the population density estimation, although it may be suitable for other objectives, such as the compilation of a reliable mammal species list (Tobler et al. 2008; Vanthomme et al. 2013; Cusack et al. 2015) or the remote observation of specific behaviours or interactions (Pebsworth et al. 2012; Boesch et al. 2017; Smith et al. 2020). This design violates the assumption that cameras are placed randomly to the animal's spatial distribution. Suppose we placed all cameras along animal trails. In that case, the estimated staying time may be shorter, and the number of passes may be much larger compared to the survey area's average. Surveyors may, therefore, obtain a severely biased density estimate.

Opportunistic placement refers to a sampling design where cameras are placed solely based on surveyors' own experience and intuition—this is not a design. If the design isn't explicitly determined or reported, one cannot judge the survey's reliability or replicate it.

Select a camera trap model

With the rise of camera trap research, many companies offer a vast range of camera models. The overwhelming choice leaves us at a loss as to which model from which company to buy. Some websites, such as "trailcampro.com" (https://www.trailcampro.com/), offer data comparing and evaluating many camera trap models and can help you choose camera models. Research papers often specify the model used. Some studies compared the performance of different cameras (Apps & McNutt 2018a). Informal advice from colleagues and social networking sites may also

be useful. Here, we focus on the minimum requirements for our purposes.

The video mode is an essential feature when using the REST model, which requires measuring animal staying time in the detection zone. High video quality is not necessary since the REST model doesn't need individual identification. Alternatively, continuous still photography may be used to measure the staying time, but with fast-moving species, the entry and exit of the detection zone are often missed. Videos are also helpful for species recognition among similar species (Hongo et al. 2020).

Fast trigger speed and minimum (<1 s) time interval option are highly recommended to avoid many censored staying time. Right-censored staying time data can be incorporated into the model (Nakashima et al. 2018), but the less such data, the better. Moreover, it is challenging to manage left-censored data—staying time where the entry into the detection zone was not observed—so we prefer cameras that start recording instantly on detection.

A small built-in display is very useful for checking a camera's field of view and adjusting its angle and position. The REST model assumes the perfect detection of the focal species within the detection zone (Table 1), so standardising the camera angle and position in relation to the detection zone is crucial.

Infrared flash LEDs, particularly "low-glow" and "no-glow" LEDs, are highly recommended to avoid altering the behaviour of detected animals. White LEDs are suitable for capturing clear images but may disturb animal behaviour and bias the staying time.

If it's possible to use the time-lapse mode simultaneously as the motion-trigger mode, one should do so. This is not mandatory, but analysts can accurately calculate the survey period if cameras automatically take one video every day at midnight.

Configure camera setting

We have now selected and purchased camera traps best suited to the survey. The next step is to make some settings as described below. Once you have completed these settings, we strongly recommend testing the cameras before going to the field with them.

As discussed in the previous section, cameras need to be set to the video and motion-trigger modes. If your cameras allow using the time-lapse function concurrently with the motion-trigger mode, please set to take one video footage every day at 00:00. Video length should cover the whole staying time: A length of 20–30 s seems sufficient for many species. Moreover, the time interval from the previous video must be minimal. Lastly, it is better to make your cameras work 24 hours even your subjects are strictly diurnal or nocturnal, as animals often exhibit some extent of cathemerality, which may be not yet known even by experts.

Lay out the camera station

The data quality in the camera-trap survey strongly depends on the layout of camera-trap stations. Even if we have carefully planned the placement design and selected a suitable camera model and configuration, a major mistake in the layout can render all the efforts worthless. This section discusses the layout considerations and two recommended examples.

There are three basic rules. Firstly, modification of the environment around the stations should be as minimal as possible. Placing baits or lure isn’t an option, and you should try to leave as little human scent as possible around the stations. The undergrowth in front of cameras should be cleared to ensure perfect detection. But it

may also alter the behaviour of sensitive species, so the clearing area should be standardised and kept minimal.

Secondly, the detection zone needs to be standardised so that every camera detect the focal species with certainty. Therefore, surveyors have to determine the zone within which the focal species can be certainly detected by testing with animals of comparable weight. This test should be carried out before the start of your survey. The zone can be any shape, as long as it ensures certain detection, but we recommend an equilateral or isosceles triangle. The zone's appropriate shape, size and distance from the camera depend on the camera model.

Lastly, it is advisable to orient cameras to the north or south. Easting and westing cameras will cause sensors to trigger morning or evening sunlight, resulting in plentiful "empty" videos.

Below, we present two examples of station layouts that will be useful for surveys in forested areas. The first example is the most typical and commonly used; the second one may be more suitable if there's a concern that animals avoid cameras or camera stations or destruct cameras.

Horizontal layout

The most general layout involves fixing a camera trap at the shoulder height, or slightly lower (Apps & McNutt 2018a), of focal species and orienting the camera so that its view is parallel to the ground (Fig. 3a). Note that we should adjust the camera height and angle based on the ground at the detection zone, not the ground directly below the camera (Fig. 3a-iii, 3a-iv). When setting the detection zone's size and distance to the camera, you have to make sure the two points (Fig. 3a-ii): Does the camera's view cover the entire detection zone?; Does the animal always trigger the

camera sensor, no matter which direction it enters the zone?

In this layout, the horizontal orientation of camera traps leads to a long detection range. This allows us to set a wide detection zone, which increases the sample size of staying time. Although the sample size of the number of passes doesn't depend on the detection zone's size, the mean density may be estimated more precisely if the number of cameras with zero detection is reduced. This layout, however, possibly have a large impact on animal behaviour. The camera height has to be low because of the horizontal orientation, typically 30–50 cm above the ground. So, surveyors have to clear a considerable area—from the camera to in and around the detection zone—of undergrowth almost from the base (Fig. 3a-i). This may discourage vigilant animals from entering the zone or alter their travel speed within the zone (Caravaggi et al. 2020). Moreover, the detection zone may be squashed vertically flat in the video images, making it difficult to measure the staying time in subsequent video analysis.

Depression-angle layout

In areas where animals are sensitive to the presence of camera traps, human odours on the cameras, or cleared undergrowth, the horizontal design may alter their behaviours and cause considerable bias in sampling. When surveying in such areas, the best way is to adopt another station layout where the cameras are fixed at a higher position and face downwards at an angle (Fig. 3b). When surveying a mammal with a shoulder height of about 50 cm, for example, it may be suitable to set cameras at 100–120 cm above the ground to keep them out of sight. As with the horizontal design, we have to standardise the camera's position relative to the detection zone and test for perfect detection within the zone (Fig. 3b-iii, 3b-iv).

In this depression-angle layout, the detection zone triangle will be more visible in videos than in the horizontal layout (Fig. 3b-ii), allowing analysts to measure the staying time accurately. It also results in minor vegetation disturbance because there's no need to uproot the grass and vines that block the space between the camera and the detection zone (Fig. 3b-i). This layout is, however, more difficult to be standardised to guarantee perfect detection. Hence, surveyors have to carefully test the detection certainty and receive training to replicate the same layout at all the stations.

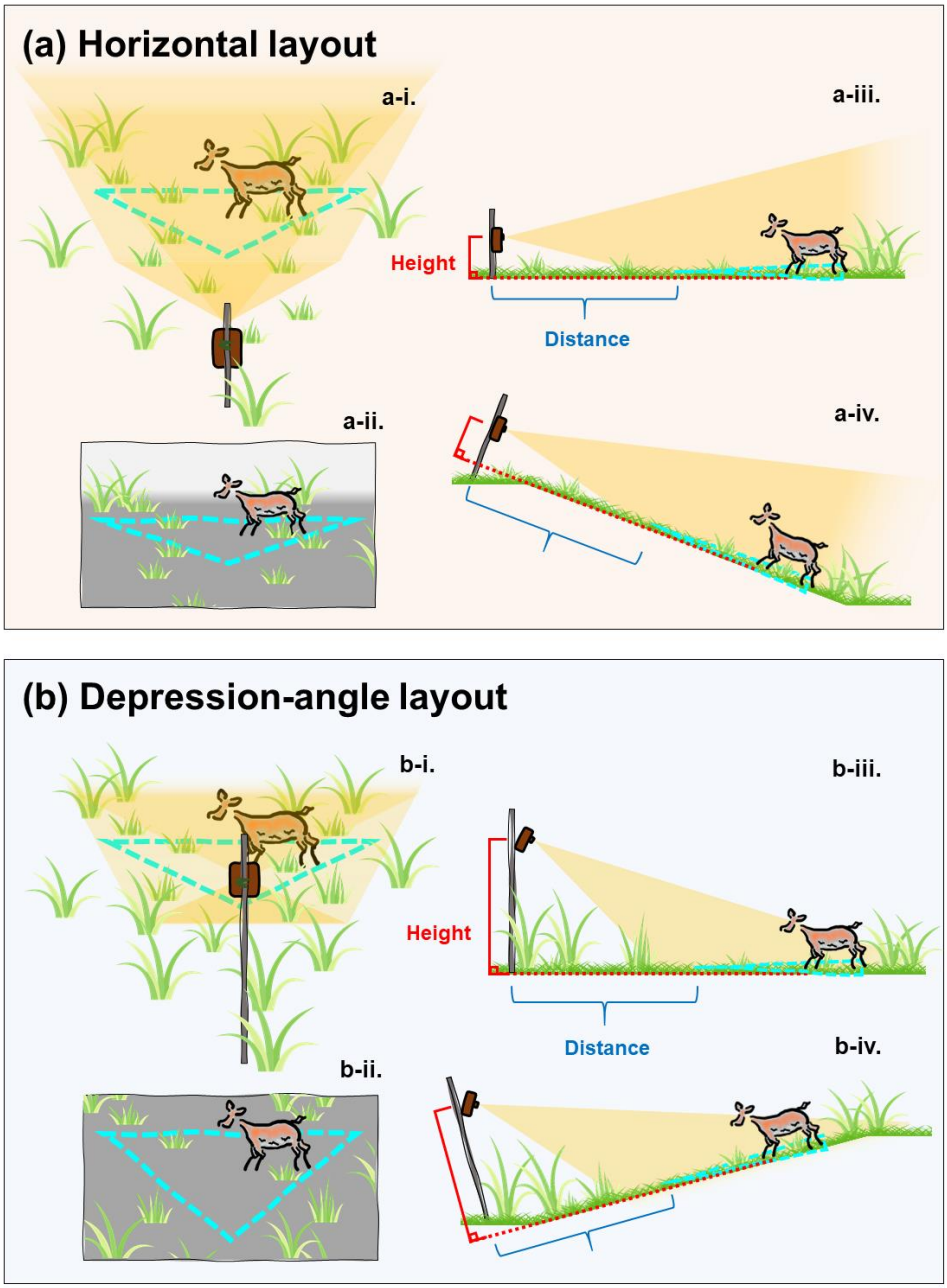


Fig. 3 Schematic images of (a) horizontal and (b) depression-angle layouts of a camera station. Images (a-i) and (b-i) show views from the back of the camera trap. Images (a-ii) and (b-ii) depict images on the built-in display. Images (a-iii) and (b-iii) represent side views of the stations where the ground is level; images (a-iv) and (b-iv) represent those where the ground is tilted. In each image, the dashed blue triangles show the detection zone.

List the covariates

If the objective is simply to estimate the mean density of the survey area, this section can be skipped. By contrast, if the aim is to incorporate habitat covariates into the model, which potentially explain variations in staying time and density, you need to obtain them for each station. These covariates have to be extrapolatable to entire the survey area; otherwise, it will be impossible to predict the density distribution over the entire survey area. Therefore, the covariates will not be measured at the station when the camera is installed but should be obtained in advance from appropriate maps and GIS databases. Environmental covariates include elevation, slopeness, vegetation types, and the distance from the forest edge; anthropogenic ones include the distance from settlements, human population size in the settlements, and administrative zones (e.g., logging zone, natural reserve). A set of covariates influencing staying time and density will vary between the species and survey area. Thus, to decide on candidate covariates and methods to measure them, surveyors have to wade through the literature to know the ecology of the focal species and the history and characteristics of the survey area.

Carry out the survey

Good survey plan developed—let's go out into the field. Before entering the forest, the survey team should establish a proper schedule. An unrealistic field plan will lead to mistakes and, above all, unexpected illness and injury. Prepare the survey equipment carefully. List all the necessary supplies (e.g., ropes for marking the detection zone, measuring tapes, camping stuff, food, first aid kit, among others) and number each

camera after the operation check. Batteries and SD cards should be installed in the camera before going to the field to save labour at the camera stations—don't forget to turn off the power.

In the field, surveyors use handheld GPS devices to reach predetermined camera station points. Arriving at a point, we should take care not to arbitrarily determine the camera place. The GPS devices have a positioning error of 5–10 m, so there is a risk that we unintentionally choose an open area. To avoid this, we have to mechanically select the point where the GPS navigation system first indicates that the distance to the destination became 0 m. Instead of fixing a camera to a tree nearest the point (this would also bias the sampling), it's better to drive a picket into the point and strap the camera to it.

Establish the camera station according to the layout you planned. On your datasheet, record the time and date of installation and the required measurements. Then check if the camera station is appropriately prepared as you planned: Is the detection zone well within the camera's field of view (Fig. 4a, b)?; Is the camera appropriately triggered when an animal enters the zone?; Are there no obstructions—herbs, vines or tree brunches—between the camera and the detection zone (Fig. 4c, d)? If even a tiny leaf is right in front of the camera, it will be exposed to the infrared flash, probably making night-time videos completely dark (Fig. 4e, f). Even if the camera view is unobstructed at the time of placement, over time, herbs will grow, and vines will hand down due to wind and rain, which should be anticipated and removed beforehand. When all checks are complete, take one "empty" video (or photo) with the detection zone string in place, after which we remove the string and leave for the next station.

Fig. 4 Captured images of camera trap videos. Camera stations with ropes defining the detection zone in (a) a horizontal and (b) a depression-angle layout. Analysts use photos of this kind to measure the staying time. If the camera's field of view is obstructed by (c) leaves or (d) a tree branch, the perfect detection assumption is not met, and the staying time also cannot be correctly measured. Besides, if a tiny vine is in front of the camera, (e) daytime videos are recorded without problem, but (f) night-time videos are darkened by the flashes illuminating the vine, making it very difficult to observe detected animals—there is an Emin's giant pouched rat, *Cricetomys emini*, in the centre of the image.

What if we can't reach the station because of a river or a cliff? The first option

is to find a diversion and manage to get there. But sometimes, the point indicated by the GPS is in a large river or a deep valley. In that case, we need to shift the point, but there's again a risk of introducing arbitrariness. To prepare for such cases, it might be a good idea to have second points for all the stations in advance or make a rule such as "place the camera at the point 100 m north of the original".

Analyse the data

Data acquisition from videos

Species identification

Faced with the obtained data set containing thousands, or tens of thousands of videos, analysts first have to do "tagging" (identification of animal species recorded). Many recent researchers develop image recognition programs using deep learning (Norouzzadeh et al. 2018; Willi et al. 2018). There are also projects, such as Wildlife Insights (https://www.wildlifeinsights.org), which automatically tag animal images uploaded to websites. Most of these programs, however, work only for photos and not for videos. Therefore, at least for the moment, this task has to be done manually by analysts, one by one. If you only want to estimate the density of particular species, videos of the other species may be skipped. But you may think that this is a terrible waste of data. In that case, analysts have to identify species of each video using appropriate nomenclatures, such as Kingdon (2015) and Francis (2019).

Brave analysts may be planning to complete this painful task using a media player (such as VLC media player) and a spreadsheet (such as Microsoft Excel or Apple Numbers). But this will result in dubious datasheets, contaminated by numerous human errors, after hundreds of hours of work. We should avoid this risky "media

player–spreadsheet" approach; otherwise, our careful planning and hard fieldwork may go to waste. Instead, analysts can use software that supports video tagging. Among several alternatives, including Aardwolf (Krishnappa & Turner 2014) and ViXeN (Ramachandran et al. 2018), we recommend Timelapse (Greenberg et al. 2019; Greenberg 2021). This free software is fast, accepts videos (.mp4, .avi and .asf), has flexible tagging options, easily converts the tags to a CSV file, and is still being updated, although it only works on Windows OS.

After the necessary species identification work has been completed, it's advisable to publish, if possible, a video list of the identified animals—this is important to ensure the validity of the analysis results and as a reference for those working in the same area. We provide a video list of mammal videos recorded in southeast Cameroon on our YouTube channel (https://www.youtube.com/playlist?list=PLAxagdZwt_bmmYkZlcDjnpCaBm1Nvk1aY).

Measurement of necessary values

Once the hard work of species identification is done, analysts have to dive into another hard work—the measurement of values required in the REST model. The values are:

(1) survey period (number of camera working days),

(2) the number of animal passes at each station,

(3) staying time of each detection, and

(4) time of animal passes.

We can calculate the survey period of each camera station from the field note and the camera recording history. The other three values are obtained from videos, so analysts can use Timelapse or equivalent software to record them. The time of animal passes is

automatically recorded in the video files. In contrast, the number of passes and staying time must be visually recorded from videos. For this purpose, we need to make the window showing the detection zone photo semi-transparent and superimpose it on the animal video images on a computer display (Fig. 6). The authors use TranspWnds (https://code.google.com/archive/p/transpwnds/downloads) to transparentise windows, but there appear several alternatives. For measuring these values, analysts have to define, in advance, the reference body part (e.g., the right hind leg toe).

Statistical modelling

After the data acquisition from camera trap videos, statistical modelling using the data—the most exciting but often depressing part of the wildlife survey—awaits you. The statistical analysis details on the REST model are provided in previous papers (Nakashima et al. 2018; Nakashima et al. 2020), so we give here only several essential points.

First, before struggling with the modelling, carefully check the data organisation to remove human error from the data. Are staying time values calculated correctly, particularly when one stay spans several videos? Do the numbers of passes match the number of staying time data for all the stations? Did you exclude periods when the camera was malfunctioning from the survey period?

Second, we recommend constructing the REST model as a Bayesian statistical model, rather than a frequentist model, using Stan (Stan Development Team 2021) or JAGS (Plummer 2017). Bayesian modelling is much more flexible, and we can easily estimate the expected values and their credible intervals of the population density and its covariates.

Discussion

Estimating animal density is central in population ecology and wildlife management, yet difficult to achieve, particularly in forested areas. Camera traps have the potential to overcome this challenge but need to be used with an appropriate method to get accurate estimates. In this report, we overviewed the practical steps involved in estimating the density using camera traps. We have described the steps assuming the use of the REST model, but many parts of the report will also be helpful when applying other models. The keys are to correctly understand the structure and assumptions of the model we use and to plan a survey accordingly. Generate a placement design that meets the assumptions, select a suitable camera model, check the setting, and finalise the camera station layout after tests in the laboratory. Once you have finished a detailed research plan in place, then carry out the survey as closely as possible to the plan. After retrieving cameras, a large amount of video data awaits the analysts. Analyse the videos efficiently and perform the statistical modelling accurately.

Planning a camera trap survey can sometimes be a lonely task. In the planning process, however, we are often confronted with details that cannot be decided alone. God is in the details, but so is the devil. So share and discuss your draft with your collaborators and colleagues, then revise the plan. Moreover, we hope more camera trappers share their survey plans in their articles and reports (Meek et al. 2014). If it's not possible to include the detailed methods in a research paper, it may be shared on open access platforms, such as preprint repositories (e.g., bioRxiv, https://www.biorxiv.org/) and social networking sites (e.g., ResearchGate, https://www.researchgate.net/). These practised protocols will undoubtedly be helpful

to others planning new surveys, as well as proving that your findings are robust. We hope that our practical guide will not remain isolated but rapidly becomes “one of many”.

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