Camera Trap Monitoring for Wildlife Density Estimation with the REST Model

A Handbook Focusing on Rainforest Mammals

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Further information

Supplementary materials are available at:
https://sites.google.com/kyoto-u.ac.jp/comeca/camera-trap-handbook

Project websites:
https://sites.google.com/kyoto-u.ac.jp/comeca/english
https://www.youtube.com/channel/UCFuAzBCtF-gTiocvKbNDA0g **(YouTube Channel)**

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1. Introduction

Why Camera Traps, and Why Population Density?

How can we accurately estimate the population density of wild animals? How can we reliably assess the spatial differences in the density between several areas? These questions are commonly important for people engaging in wildlife monitoring, including field ecologists, conservation officials and area managers (Elliot & Gopalaswamy 2017; Burgar et al. 2018; Santini et al. 2018; Cavada et al. 2019). Tropical rainforests have many biodiversity hotspots (Myers et al. 2000; Marchese 2015; Hu et al. 2021), where the global community has a strong conservation interest. Due to poor accessibility and visibility, however, wildlife managers in rainforest areas have long faced difficulties in effectively estimating animal density.

Suppose that, for example, you decided to estimate the abundance of a terrestrial, solitary mammal species in a 5 x 5-km rainforest plot using the **line-transect distance sampling**, a conventional method still popular in rainforest areas (Buckland et al. 2015) (Fig. 1a). And suppose that the true abundance of 10 individuals/km^2 was unknown to you. You would systematically open 10 line transects of 1 km in the plot. The plot had thick undergrowth, so the effective stripe half-width was 15 m, we suppose. In this scenario you would need to walk a total of *ca.* 200–267 km along transects before obtaining 60–80 observations (the minimum number of observations required for reliable estimation of the distance function (Buckland et al. 2001)). Even if you could walk four transects a day, at least 50–67 days would be required to estimate the density in this small plot—that's too hard, too inefficient work.

Camera traps—motion-triggered automatic cameras with (often passive infrared) sensors (Apps & McNutt 2018b)—have been introduced into rainforests as a powerful monitoring tool to solve this conundrum (O'Connell et al. 2011; Burton et al. 2015). Although camera trap monitoring requires a relatively high initial investment, it has a major advantage in labour costs. Camera trapping is also less invasive for vegetation and animals than most conventional methods. There is no need to cut transects in the forest or observe animals directly. Consequently, camera trapping has become a standard method for forest mammal surveys (McCallum 2013).

Let's use again the small-plot scenario exemplified in the two paragraphs above to illustrate the efficiency of camera trapping (Fig. 1b). Now, you would need to leave 25 camera traps in the forest for about 40 days. Fieldwork is necessary only when the cameras are placed, checked for operation (every 2 to 4 weeks) and retrieved. A skilful manager will install about 4–5 cameras per day, thus finishing the installation in 5–6 days. Then it would take 4–5 days for camera checking and another five days for the retrieval. So, your fieldwork would take only 13–16 days, about one-fourth the time required in the line-transect distance sampling.

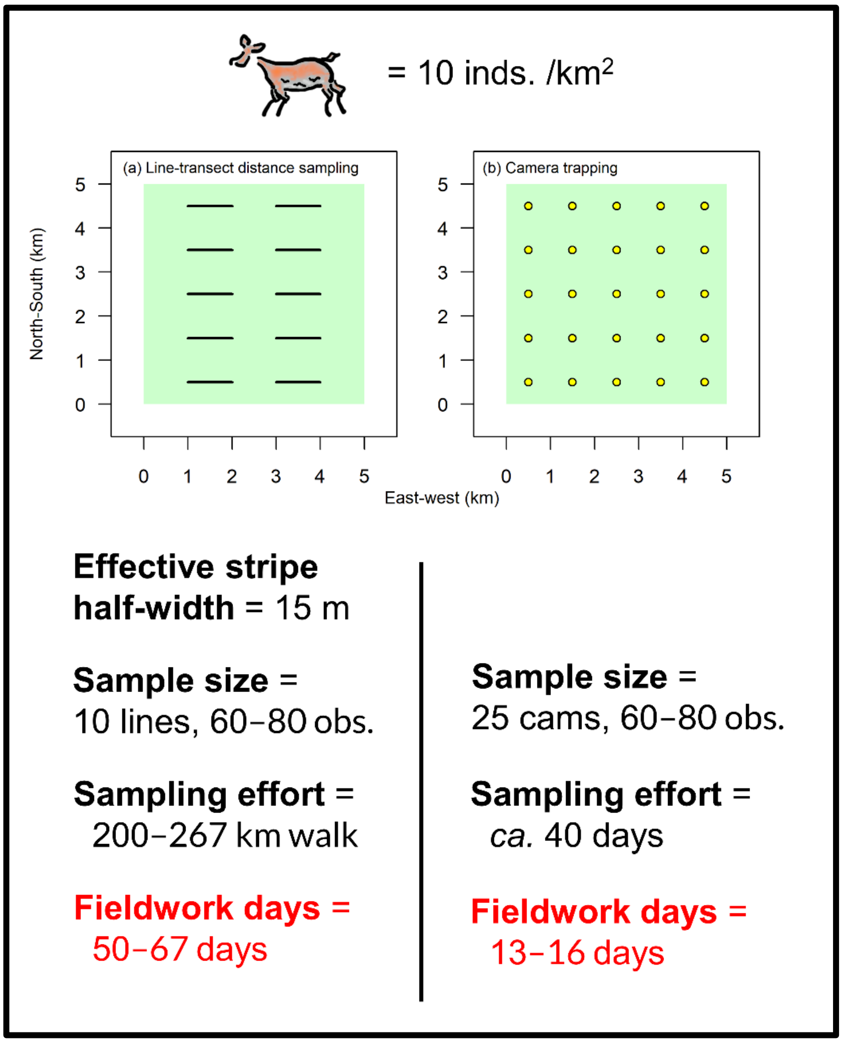

Fig. 1 Virtual monitoring plans for density estimation of a population with a true density of 10 km^{-2}, using (a) line-transect distance sampling and (b) camera trapping.

Using the Detection Rate is "a Risky Business"

After leaving the cameras for weeks, wildlife managers will obtain hundreds or thousands of images. But how can they estimate the abundance of the target species from the image data? The **detection rate**—the number of times a camera observed the target species' individuals divided by the number of days the camera was operational—is a simple index that may imply relative animal abundance (Carbone et al. 2001). Because of its intuitive and easy-to-calculate nature, the detection rate is called the **relative abundance index (RAI)** and has been used widely in wildlife monitoring.

Inferring animal abundance with the detection rate is, however, now considered a “risky business” (Sollmann et al. 2013). This is because the detection rate is affected not only by animal abundance but also by several other parameters, such as the detection probability of camera traps and animal behaviour.

Suppose, for example, that the camera sensor range is larger in the day than at night, as observed in a Panamian forest (Rowcliffe et al. 2014). In that case, a diurnal species will mark a higher detection rate than a nocturnal species of the same abundance. Similarly, the sensor range and the camera’s field of view are considerably different between makes and models (Apps & McNutt 2018a), making it difficult to directly compare the RAIs between projects. Also, the detection probability at a given distance generally increases with the body mass of the target species. So, large species may provide a higher detection rate than small species of the same abundance.

The movement behaviour of animals also affects the detection rates. Animals moving fast or active for a long time can encounter cameras more often than slower or inactive animals. This poses a problem for inter-population comparisons because a species can often display different movement behaviours based on habitat types and the extent of human disturbance. For example, populations suffering from a high hunting rate may become more vigilant and travel more slowly. If this is the case, the detection rates of these populations will be low compared to those without hunting risk, even when the former populations are as abundant as the latter.

Estimating the Population Density of the “Unmarked” Animals

Field ecologists now agree that the **population density**—the number of individuals living in a unit area—is the most appropriate index for comparing animal abundance between species and populations and for monitoring temporal changes in the abundance. And researchers have proposed several statistical models to estimate the density from the camera trap data (Gilbert et al. 2021). Some of them are only applicable for “marked”, individually identifiable species (e.g., large- to medium-sized carnivores), whereas others can also be used for “unmarked” species. The latter models include the **Random Encounter Model (REM)** (Rowcliffe et al. 2008), the **Spatial Count (SC) model** (Chandler & Royle 2013), the **Camera Trap Distance Sampling (CTDS)** (Howe et al. 2017) and the **Random Encounter Staying Time (REST) model** (Nakashima et al. 2018), among others.

The REST model

The REST model is one approach to estimating the density of unmarked animal populations exclusively from camera trap data. Nakashima et al. (2018) first proposed this model and applied it to forest duikers, demonstrating that it produced similar densities to the conventional line-transect distance sampling. REST was subsequently tested using human volunteers and simulated camera trap surveys, yielding unbiased density estimates regardless of changes in human abundance (Garland et al. 2020). More recently, Palencia et al. (2021) compared the performance of REM, CTDS and REST using Spanish wild mammals and found that the three models provided accurate estimates in most situations. They also concluded that REST **requires the least time in analysis** among the three models and is recommended for populations with **relatively high abundance**. Another advantage of REST is that it has been developed as **a likelihood-based model**, which allows investigating spatial differences in animal density by incorporating habitat covariates into the model (Nakashima et al. 2020; Yokoyama et al. 2020).

On the other hand, REST has some assumptions to ensure unbiased density estimation. So researchers and practitioners need to understand them thoroughly before making their monitoring plans. Research papers cited above can be referred to establish the plans, but field and analytical procedures are not fully provided in these papers. A preprint by Nakashima et al. (2021) is a valuable guide for practitioners who have some experience in camera trapping and are looking to use REST for wildlife monitoring. Here, we instead provide a protocol for beginners who are relatively inexperienced in camera trapping and unfamiliar with statistics. Reflecting on our own experience, this manual assumes terrestrial mammal species in tropical rainforests (e.g., forest ungulates and large rodents) as monitoring targets. We first explain the formula and assumptions of REST briefly. Then, we describe the field and analytical procedures required for density estimation with REST.

2. The REST model: A Brief Explanation

Formula

The REST model formulates the population density at a camera's focal area (D_i) as follows:

$$\mathbf{D}_i\ (\mathbf{km^{-2}}) = \frac{[\mathbf{Number\ of\ Detections}_i] \times [\mathbf{Mean\ Staying\ Time\ (s)}]}{[\mathbf{Camera\ Operation\ Time}_i\mathbf{(s)}] \times [\mathbf{Activity\ Level}] \times [\mathbf{Focal\ Area\ (km^2)}]}$$

Here, the **activity level** is defined as the average proportion of active individuals (i.e., individuals moving on the ground) among the population, ranging from 0 to 1. The **focal area** is where the camera certainly detects passages of the target species. Finally, the **mean staying time** is the mean of time the target species' individual stays in the focal area during a passage.

How to derive this equation is explained in detail elsewhere (Nakashima et al. 2018; Nakashima et al. 2021). So instead, I aim to give a simple, qualitative understanding of what this equation shows. Firstly, the equation shows that, the other parameters being the same, a longer mean staying time (i.e., slower mean travel speed) and a lower activity level will both result in an increased population density. So, REST considers that the increased travel speed and activity of the target species will enhance the detection rates. This enables us to directly compare the abundance between species or populations displaying differential movement behaviour. Secondly, REST requires that the detection of the target species within the focal area is perfect. Therefore, we can compare the estimates between different projects using different camera makes or models, provided that this assumption is met.

Assumptions

REST has the following six assumptions:

(1) Close population—The abundance of the target animal population should be stable throughout the monitoring period. This assumption suggests that one monitoring period has to be sufficiently short (e.g., 2 to 3 months) to avoid the growth, depletion and migration of the target population during the period.

(2) Random camera placement—Camera traps should be placed randomly with respect to animal behaviour. This assumption suggests that one must not intentionally place cameras where animals are likely to pass frequently or stay for a longer time (e.g., along with animal trails, at waterholes and mineral licks); such targeted placement may positively bias the density estimates. Likewise, one must not deliberately avoid places where the target animals are very unlikely to pass. Even if you find that a predetermined camera point is in a deep swamp or thick bush, you shouldn't easily give up placing a camera there—just give it a try!

(3) No animal response to cameras or camera stations—Camera traps should be placed so as not to affect animal behaviour or movement. This assumption suggests that one must not use baits or lures at camera stations. Moreover, animals in remote areas can exhibit neophilic or neophobic responses to cameras (Kalan et al. 2019); contrarily, animals in hunting areas can be vigilant to human odour left at camera stations. Environment modifications at and around camera stations must therefore be minimal. Nevertheless, this assumption can be relaxed by excluding the staying time (but not the number of detections) of responding animals from the data set.

(4) Independent observations—Observations (Number of detections and staying time) obtained by camera traps should be independent of each other. This assumption suggests that cameras should be sufficiently far apart from each other. How far is "sufficient" is a difficult question, but we often use, as a rule of thumb, the home range radius of the target species as a minimum interval between cameras.

(5) All animals being active at the activity peak—This is a requirement to estimate an accurate activity level (Rowcliffe et al. 2014). The proportion of active animals can vary with time, but all individuals in the population should be active at least at a peak. Although this assumption is considered to be met in many terrestrial mammals, semi-arboreal species may violate it because the time when each animal is on the ground (i.e., "active" in our context) will not be synchronised. Many cathemeral mammals will also fail to meet this assumption. Any severe violation of this assumption results in overestimating the activity level and hence underestimating the density.

(6) Certain detection and exact staying time measurement—As described above, REST assumes that cameras certainly detect all passages within the focal area without delay. It also assumes that the staying time is measured accurately, although the right-censored staying time (where the leave from the focal area was not observed) can be corrected statistically (Nakashima et al. 2018). The violation of these assumptions leads to an underestimation of the density. To meet them, managers have to choose an appropriate camera model and conduct rigorous field tests before determining the **camera station layout**—the focal area's size and shape and the camera's position in relation to the focal area.

Additionally, when one intends to use a likelihood-based approach to estimate the density, **(7) the**

number of detections and staying time are assumed to follow given parametric probability distributions.

Assumptions 1 to 5 are shared with CTDS and REM (if animal travel speed is estimated separately from camera trapping, REM doesn't require Assumption 5) (Palencia et al. 2021). Conversely, these two models don't require Assumption 6 but instead assume certain detection at 0 distance from the camera (Rowcliffe et al. 2011), similar to the observational distance sampling.

Limitations

A limitation of REST is the low applicability in a scenario where a low-density species is monitored with limited sampling efforts. Since REST considers only animals that crossed a small focal area, the expected detection rate can be not enough to obtain precise estimates in this scenario, as Palencia et al. (2021) pointed out.

In addition, the applicability of REST for group-living animals is not yet rigorously tested. Although Nakashima et al. (2018) obtained unbiased density estimates for simulated pair-living animals, the effects of larger group size on the estimation accuracy and precision remain unknown. Theoretically, the precision of the mean staying time estimate could be underestimated in large-group situations because the staying time would be mutually dependent between individuals in the same group.

Suitable and Unsuitable Situations for REST

I summarise below the animals for which applying the REST model is suitable and unsuitable.

Suitable species or populations are:

- Terrestrial;
- Living in solitary (or pairs);
- Medium- to large-sized (e.g., >1–2 kg);
- Synchronising the activity rhythm (many diurnal and nocturnal mammals will meet this assumption);
- Living with a medium to high abundance;
- Not exhibiting large-scale migration in a short period; and
- Rarely responding to camera traps.

By contrast, unsuitable species or populations are:

- Semi-arboreal;
- Living in large groups;
- Too small to ensure the certain detection within the focal area (REM or CTDS may be more suitable for this scenario);
- Not synchronising the activity rhythm (e.g., cathemeral mammals);
- Living with a low abundance (CTDS may be more suitable for this scenario);
- Exhibiting large-scale migration in a short period; and
- Often responding to camera traps and camera trap stations.

To our knowledge, many solitary or pair-living ungulates, medium-sized carnivores, and medium-sized to large-sized rodents living in rainforests will meet all the conditions above. By contrast, REST may not be applicable to large carnivores (often cathemeral and too scarce), primates (semi-arboreal and group-living) and small rodents (may not ensure the perfect detection in the focal area) living in rainforests, for example.

Conclusively, field managers should carefully assess if their target population meets these suitable conditions before planning the camera trap monitoring with REST. If the population severely violates a condition, one should consider whether monitoring objectives can be fulfilled by using another density-estimation model or estimating the occupancy (MacKenzie et al. 2017) instead of the density.

3. Development of REST Monitoring Protocols

Following careful consideration, if the REST model is found to be suitable for the target population, then the manager will develop a monitoring plan. At this point, building each part of the protocol to meet the assumptions of the REST model is essential. The following points are of particular importance:

- **Camera specs**—Is your camera model resistant to moisture in the forest? Does it have a battery life of at least one month? Does it have a video recording mode or a continuous photo shooting mode? Is its "trigger speed" fast and stable enough? Is its minimal time interval between recordings short? If possible, does it have a built-in display?
- **Camera placement design**—Is the number of cameras or camera stations large enough to estimate the density precisely? Does your camera placement design meet the REST's assumptions? Isn't it too tough for your team to install all the cameras according to your design?
- **Layout of the camera station**—Is the camera position (height, orientation and distance from the focal area) determined based on the field test for satisfying the certain detection assumption? Are the shape and size of the focal area too? Does this layout prevent the target animals from reacting frequently?

Required Specifications of Camera Traps

With the rise of camera trap research, many companies offer a vast range of camera models. But the overwhelming choice leaves us at a loss—which model should we buy from which company? Some websites, such as ***Trailcampro* (https://www.trailcampro.com)** and ***Trail Camera Lab* (https://www.trailcameralab.com/)**, provide reviews of many camera models with the spec information and customer opinions, which will help to select appropriate models. Additionally, advice from your experienced colleagues and social networking sites may be beneficial.

Here, we focus on the minimum requirements for applying the REST model. First, the camera used for REST should have **the video recording mode**, which allows for measuring animal staying time accurately (Assumption 6). Videos are also helpful for species recognition among similar species (Hongo et al. 2020). Alternatively, **the consecutive photo shooting mode**, where the camera takes 3 to 10 photos continuously after a single trigger, is also acceptable if the exact time is recorded for each shot.

Second, **fast trigger speed** (≤1 s) and **minimum time interval** (≤2 s) options are required to ensure the certain detection and accurate staying time measurement (Assumption 6). Right-censored staying time data can be statistically incorporated into the model (Nakashima et al. 2018), but a high amount of such data worsens the precision of density estimates. Moreover, it is challenging to manage the left-censored staying time, where the entry into the focal area was not observed. Therefore, the fast trigger is essential.

Third, **infrared flash LEDs** are necessary to avoid altering animal behaviour (Assumption 3). The "low-glow" or "no-glow" LEDs are more desirable but not mandatory: Cameras with these high-spec LEDs are expensive, so purchasing them will reduce the total number of cameras available. Contrarily, white LEDs are unsuitable because their strong light may severely disturb animal behaviour and bias animal detections and staying time.

Lastly, a **built-in display** is preferable if available because it helps check a camera's field of view and adjust its angle and position. This is very useful to standardise the station layout in the field.

For reference to the readers, we name a few experienced models. We currently use **Browning Strike Force HD Pro X** (BTC-5HDPX, https://browningtrailcameras.com/products/strike-force-hd-pro-x) with the video mode, the 1-s time interval and the Fast Motion setting. This model has a fast trigger speed and recovery time. It also has a built-in display. Yokoyama et al. (2020) also used a Browning's camera (Browning Strike Force HD Pro, BTC-5HDP). The original field study by Nakashima et al. (2018) used a **Bushnell Trophy Cam** (https://www.bushnell.com/trail-cameras-2/), and Palencia et al. (2021) employed **Bushnell Aggressor Trophy Cam** (https://www.bushnell.com/trophy-cam-hd-aggressor-no-glow/883505.html) to apply REST, REM and CTDS.

Camera Placement Design

An appropriate placement design is essential to meet the random placement (Assumption 2) and the independent observations (Assumption 4). Although geographic information system (GIS) software allows us to draw any placement designs, suitable designs are only part of them. Here, we introduce several suitable placement designs and some to be avoided. The Supplementary Materials provide instructions for creating suitable installation designs using QGIS.

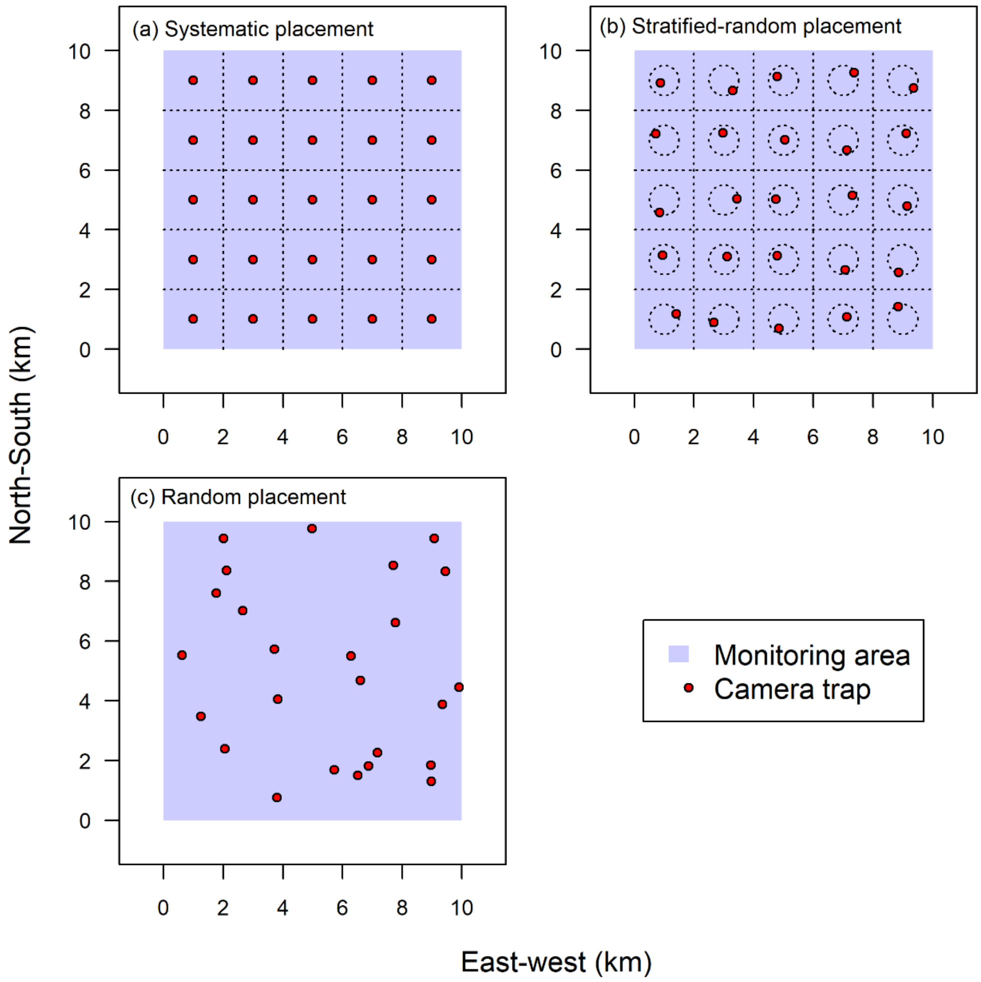

Fig. 2 Schematic maps of four suitable camera placement designs: (a) systematic placement, (b) stratified-random placement and (c) random placement (without a minimum interval between cameras). In each panel, 25 points for camera trap stations are generated in a 10×10 km monitoring area.

Suitable designs

Systematic placement is the first choice (Fig. 2a). When this placement is adopted, one typically sets up a square grid over the survey area, setting camera stations at each grid's centre or intersection. Camera station points are evenly spaced throughout the survey area in this design, so Assumption 2 is met. To satisfy Assumption 4, the grids need to be wide enough. The systematic placement is a simple design and recommended in most cases, but care should be taken to apply artificially modified areas. For example, in a logging area where roads and other structures are built at nearly equal intervals, equally-spaced cameras may bias the estimates by disproportionately sampling particular environmental areas.

Stratified-random placement (Fig. 2b) is also recommended. To implement it, one sets up a coarse square grid and then generates a random point per grid for camera stations. For Assumption 4 to be met, it is advisable to draw a circle of an appropriate size in each grid's centre and generate a random point for the camera station within it. This placement will also reduce the bias introduced in artificial areas exemplified above, although it requires a little bit higher skill of GIS to be developed.

Random placement (Fig. 2c) is acceptable. 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 design naturally meets Assumption 2. To meet Assumption 4, one can set a minimum distance between cameras. However, this placement may be impractical as the installation fieldwork tends to become labour-intensive and time-consuming, particularly in large monitoring areas. Moreover, when the number of cameras is limited, this placement is more likely to introduce a larger bias in the density estimates by chance than the systematic placement.

Designs to be avoided

Targeted placement should be avoided when working on the population density estimation. Although it may be suitable for other objectives, such as the compilation of a reliable mammal species list or the remote observation of specific behaviours of particular species, this design severely violates Assumption 2. Suppose that we placed all the cameras along animal trails, for example. In that case, the estimated staying time could be shorter, and the number of passes would be much larger than the monitoring area's average. Managers would consequently obtain density estimates that are positively biased.

Opportunistic placement refers to a sampling design where cameras are placed solely based on fieldworkers' own experience and intuition—often confounded with the random placement, this is actually quite different! Since humans have potential biases when selecting camera stations (e.g., avoiding thick bush, preferring flat terrain), this opportunistic placement cannot be equivalent to the random one.

How many cameras do we need?

How many camera stations are needed is a difficult question as it depends on the precision level a manager requires. Theoretically, the number of cameras (or camera stations) affects the precision but not the average accuracy of density estimates. And the estimation precision will be ameliorated (i.e., confidence intervals will become narrower) logarithmically with the increase in the camera numbers.

Nakashima et al. (2018) performed simulations with a homogenetic monitoring area of

3x3 km, a constant animal density of 10 km^{-2} and different camera numbers. As a result, the estimation precision was clearly improved by increasing the camera numbers to 25 cameras, provided that the total sampling effort (camera-days) is kept constant. This suggests that at least 25 camera stations should be set even for a small area. Their simulations also suggested that a monitoring plan with many cameras and a short period is better than one with fewer cameras with a long period in terms of estimation precision.

The camera station density often seen in previous studies ranges from 1 km^{-2} (one camera per 1×1-km grid) to 16 km^{-2} (one camera per 4×4-km grid). The Tropical Ecology Assessment and Monitoring Network (TEAM) uses a systematic placement design with a density of 0.5 cameras per km^2 (one camera per 1.4×1.4-km grid) (TEAM Network 2011), so it is advisable to follow it if applicable.

Tropical forests are very humid, even in the dry season. Many camera models are waterproof, but leaving them for a few months can still cause them to malfunction. It is therefore advisable to buy somewhat more cameras than the number of camera stations planned, including replacement cameras.

Layout of Camera Stations

The data quality in the camera trap monitoring strongly depends on the layout of camera stations. Even if the placement design is carefully planned and a suitable camera model is selected, a major mistake in the layout can render all the efforts worthless.

There are three basic rules. Firstly, **altering the environment around the stations should be as minimal as possible**. Placing baits or lures is not an option (Assumption 3). And it would be best to leave as little human scent as possible around the stations. Although the undergrowth in front of cameras should be cleared to ensure perfect detection (Assumption 6), it may also alter the behaviour of sensitive species. So, the clearing area should be standardised and kept minimal.

Secondly, **the focal area needs to be standardised so that every camera detects the target species with certainty** (Assumption 6). Therefore, managers must determine the focal area by testing with a domestic animal or a warmed object of comparable weight to the target species. This test should be carried out prior to your fieldwork. The area can be any shape theoretically, but all previous REST studies use **an equilateral or isosceles triangle**. The area's appropriate shape, size and distance from the camera depend on the camera model. Thus, please perform a test with your cameras instead of applying the focal area of the published study that used another 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 station layouts useful for REST monitoring in rainforests. The first example is the most typical and commonly used; the second one may be more suitable if there's a concern that animals react to cameras and camera stations.

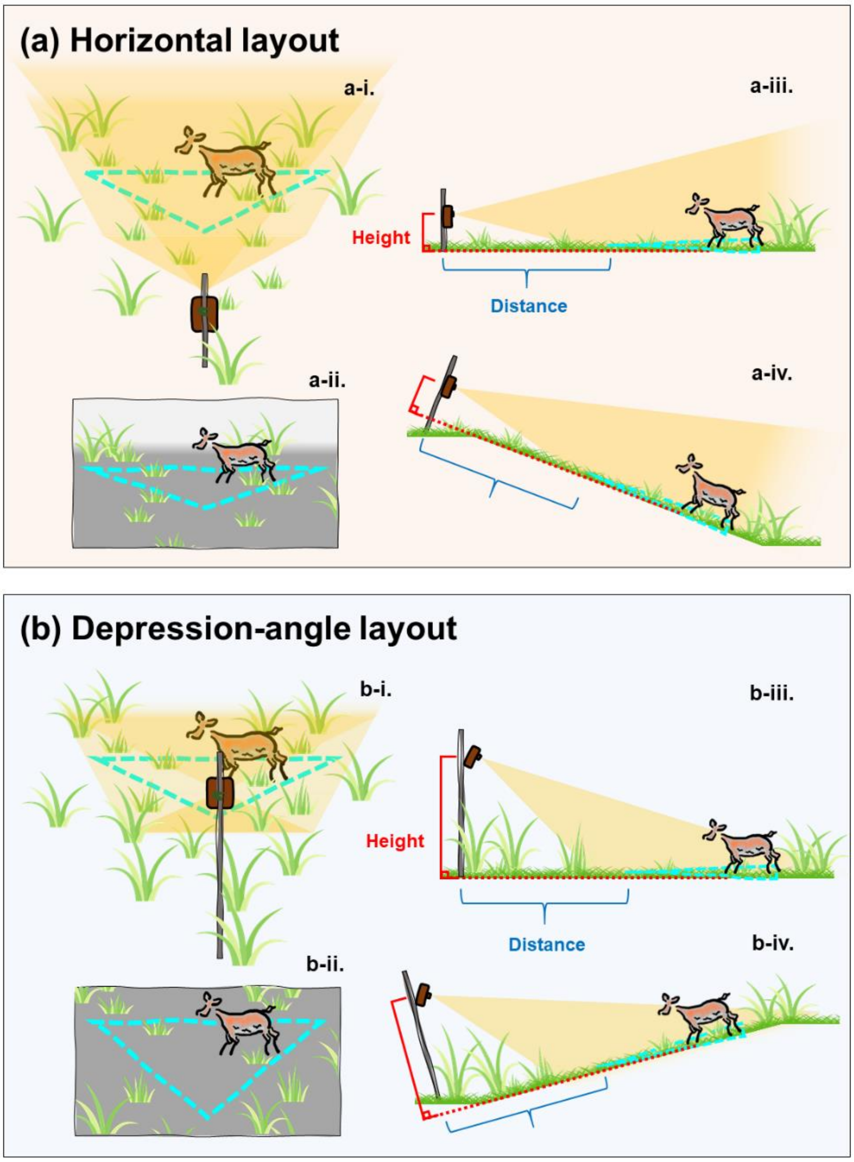

Fig. 3 Schematic images of (a) horizontal and (b) depression-angle layouts of a camera station. Images (a-i) and (b-i) show views from the back of the camera trap. Images (a-ii) and (b-ii) depict images on the built-in display. Images (a-iii) and (b-iii) represent side views of the stations where the 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.

Horizontal layout

The most general layout involves fixing a camera trap at the shoulder height of the target species or slightly lower (Apps & McNutt 2018a) and orienting the camera's view parallel to the ground (Fig. 3a). Note that we should adjust the camera height and angle based on the ground at the focal area, not the ground directly below the camera (Fig. 3a-iii, 3a-iv). When setting the focal area's size and distance to the camera, one must make sure the following two points (Fig. 3a-ii): (1) Does the camera's view cover the entire focal area?; (2) Does the animal always trigger the camera sensor, no matter from which direction it enters the area?

In this layout, the horizontal orientation of camera traps leads to a long detection range. This allows us to set a large focal area, which increases the sample size of staying time and consequently decreases the number of stations with zero detection. As a result, the mean density may be estimated more precisely. However, this layout possibly has a large impact on animal behaviour. The camera height must be low because of the horizontal orientation, typically 30–50 cm above the ground. So, the undergrowth must be cut for a considerable area (from the camera to around the focal area) from the base (Fig. 3a-i). This may discourage vigilant animals from entering the station or alter their travel speed within the focal area. Moreover, the focal area may be squashed vertically in the images, making it difficult to measure the staying time from the videos.

Depression-angle layout

If animals are sensitive to camera traps, human odours on the cameras or cleared undergrowth, the depression-angle layout may be better. In this layout, the cameras are fixed at a higher position and face downwards (Fig. 3b). When the shoulder height of the target species is about 50 cm, for example, setting cameras at 100–120 cm above the ground will be suitable to keep them out of sight. As with the horizontal layout, managers must standardise the camera's position relative to the focal area (Fig. 3b-iii, 3b-iv).

In this layout, the focal-area 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 focal area (Fig. 3b-i). This layout is, however, more difficult to be standardised. Hence, managers must carefully test the detection certainty, and fieldworkers should receive training to replicate the same layout at all stations.

One of the authors (Shun Hongo) currently uses a depression-angle layout with Browning Strike Force HD Pro X camera traps. He defines an equilateral triangle with a side of 150 cm as the focal area. The camera's height is set to 80 cm; the distance from the camera to the nearest vertex of the focal area is set to 190 m. He tested this layout with colleagues in the summer in a natural setting of Kyoto, Japan. As a result, he confirmed that the camera detected a moving object of 3.0 kg with a temperature of 40 °C almost perfectly from the entry in the focal area, no matter from which direction it entered.

4. Carrying Out the Monitoring

A good monitoring plan has now been developed—let's go out into the field! But before entering the deep forest, the monitoring team should establish a proper schedule. An unrealistic field plan will lead to mistakes and, even worse, to serious illness and injury. To ease the fieldwork and minimise the camera failure, we recommend conducting the camera placement during the long dry season, if applicable.

Materials

Prepare the monitoring equipment carefully. I list the materials needed for REST monitoring below:

- Camera traps
- Batteries
- SD cards (32–64 GB)
- Shades (to protect cameras against the rain)
- Wire (to fix cameras)
- Pliers
- Rope of the triangle focal area
- Tape measure (~10 m)
- Pink tape (to mark camera stations)
- Packing tape (to cover the battery compartment to protect cameras from moisture)
- Portable GPS devices (coordinates of camera trap stations are imported)

Configuration of Camera Setting

To save labour at the camera stations, you must install batteries and SD cards in the cameras and configure the camera setting before going to the field. Having completed the settings, I strongly recommend testing the cameras before going to the field with them. Although the configuration options and terminology vary considerably among camera models, the minimally required setting is as below:

- Motion-trigger mode (as opposed to time-lapse mode)
- 24-hour operation

- Video or continuous photo shooting
    - ✧ Video: Video length of 20–30 s
    - ✧ Continuous photo shooting: 3–10 shots
- Minimal interval between triggers: 0–1 s

Setting of Camera Stations in the Field

Leaving the research station, fieldworkers use handheld GPS devices to reach predetermined camera station points. Arriving at a point, they should not arbitrarily determine the camera place. The GPS devices have a positioning error of 5–10 m in the dense forest, so there is a risk that we unintentionally choose an open area. To avoid this, they must mechanically select the point where the GPS navigation system first indicates that the distance to the destination became "0 m" (Fig. 4a). Instead of fixing a camera to a tree nearest the point—this would also bias the sampling—it is better to drive a picket and strap the camera to it (Fig. 4c, d).

Fig. 4 The installation of camera traps. (a) Camera stations must be set at the predetermined point that the GPS device indicates, even when it is in a swamp. (b) Prior to camera installation, we set rope to define the focal area. Then, (c) we drive a picket and (d) strap a camera on it.

Establish the camera station as planned and test the camera operation by passing in front of the camera (Fig. 5a, b). Is the focal area well within the camera's field of view? Does the human passage appropriately trigger the camera? Are there no obstructions (herbs, vines or tree brunches) between the camera and the focal area (Fig. 5c, d)?

Only a tiny leaf in front of the camera can be exposed to the infrared flash, making night-time videos completely dark (Fig. 5e, 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. So fieldworkers should remove any potential obstacles when installing the camera. When all checks are complete, take one "empty" video (or photo) with the focal area rope in place (Fig. 5a, b).

Fig. 5 Captured images of camera trap videos. Camera stations with ropes determining the focal area in (a) a horizontal and (b) a depression-angle layout. Analysts use these photos 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 cannot be correctly measured. When a tiny vine is in front of the camera, (e) daytime videos are recorded clearly. But (f) night-time videos are darkened by the flashes illuminating the vine, making it very difficult to observe detected animals (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. In preparation for such cases, it might be good to create an alternative point for each station in advance or make a rule such as "moving 100 m north of the original station point".

Cameras should be checked every 2 to 4 weeks. The battery sometimes drains more quickly than expected. Wind, branches and animals may change the camera angle and position, and a spider web can cover the lens of cameras. Even worse, cameras can break down due to water accumulating inside or ants nesting in them. If these incidents are left untreated, subsequent data will be unusable, and the risk of camera failure will increase. Please visit the cameras regularly and take care of them.

After retrieving the cameras, please transfer the data in the SD cards to a hard disk as soon as possible. A subfolder for each camera should be created under a root folder for the data set, and image data will be stored in each subfolder. Subsequently, fieldworkers should take a quick look at the images and record the status of each camera and the number of days it has been in operation while memories of their fieldwork are still fresh.

5. Data Analysis

In camera trap monitoring, data analysis is often more labour intensive than fieldwork and requires knowledge and skills in statistical modelling. For density estimation with the REST model, data analysts follow the following steps:

1. Species identification
2. Judgement on whether the target species passed through the focal area
3. Measurement of staying time in each passage
4. Acquisition of time data for each passage
5. Data shaping and cleaning
6. Statistical analysis to estimate density

Steps 1 to 4 are generally referred to as image data processing, and there is a wide variety of image data processing tools. I currently use **Timelapse** (Greenberg et al. 2019; Greenberg 2021) to process the image data. This software was developed by Saul Greenberg and is freely available. It 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. But note that it only works on Windows OS. The newest version of Timelapse can be downloaded from its website (http://saul.cpsc.ucalgary.ca/timelapse/), which also provides a detailed manual of this tool. I provide a standard Timelapse template file to process the video data for REST, which is available in Supplementary Materials.

Species Identification

With the obtained data set containing thousands of videos, analysts first have to do "tagging"—identification of animal species recorded. If managers only want to estimate the density of the target species, images of the other species may be skipped. But if they feel this is a terrible waste of data, analysts can identify the species of all the videos using appropriate field guides and lists, such as Kingdon et al. (2013). In addition, since an analyst rarely has expertise in all animal taxa taken by camera traps, collaboration with experts may be required to distinguish between similar species.

After completing the species identification work, managers can report a species list of the monitoring area. Publishing videos of the identified animals will also be appreciated by other managers and researchers. This can be used as references for those working in the same region. Our project provided a list of mammal videos recorded in southeast Cameroon on the Projet Coméca YouTube channel (https://www.youtube.com/channel/UCFuAzBCtF-gTiocvKbNDA0g).

Judgement on whether the target species passed through the focal area

The number of passages in the focal area is fundamental data in REST. Analysts must visually determine whether each passage of the target species has entered the focal area. To perform this analysis, I use Timelapse, **VLC media player** and **WindowTop** (https://windowtop.info/). WindowTop lets us make windows transparent (but unfortunately does not work with the Timelapse windows).

The procedure is as follows. First, cut out a still image from the video of the focal area taken when the camera was installed (Fig. 6a). Second, highlight the rope of the focal area in the image using a paint tool, such as Paint 3D (Fig. 6b). Third, open the focal-area image with the VLC media player and transparentise this window. Fourth, superimpose the transparentised image on the Timelapse window (Fig. 6c). Lastly, play the video in Timelapse and judge the animal entries (Fig. 6d). This judgement should be based on a specific part of the animal body (e.g., the toe of the right hind leg).

When determining the animal entries, analysts should also record the response behaviour of the animals. If an animal reacted to the camera, the passage can be counted, but its staying time cannot be used for statistical analysis (Assumption 3).

Measurement of staying time in each passage

At the same time as determining the animal entries, the analysts can simultaneously measure staying time in the focal area (Fig. 6d). Also, whether each stay was right-censored (the leave from the focal area was not observed) should be recorded. Sometimes a single stay may be filmed across multiple images. In that case, analysts first need to measure the staying time of each video and then sum up them of consecutive videos, including time intervals between the videos.

Acquisition of time data for each passage

Timelapse automatically retrieves the timestamp of camera trap images. We use the time of the first image of each passage as the time of entry in the focal area.

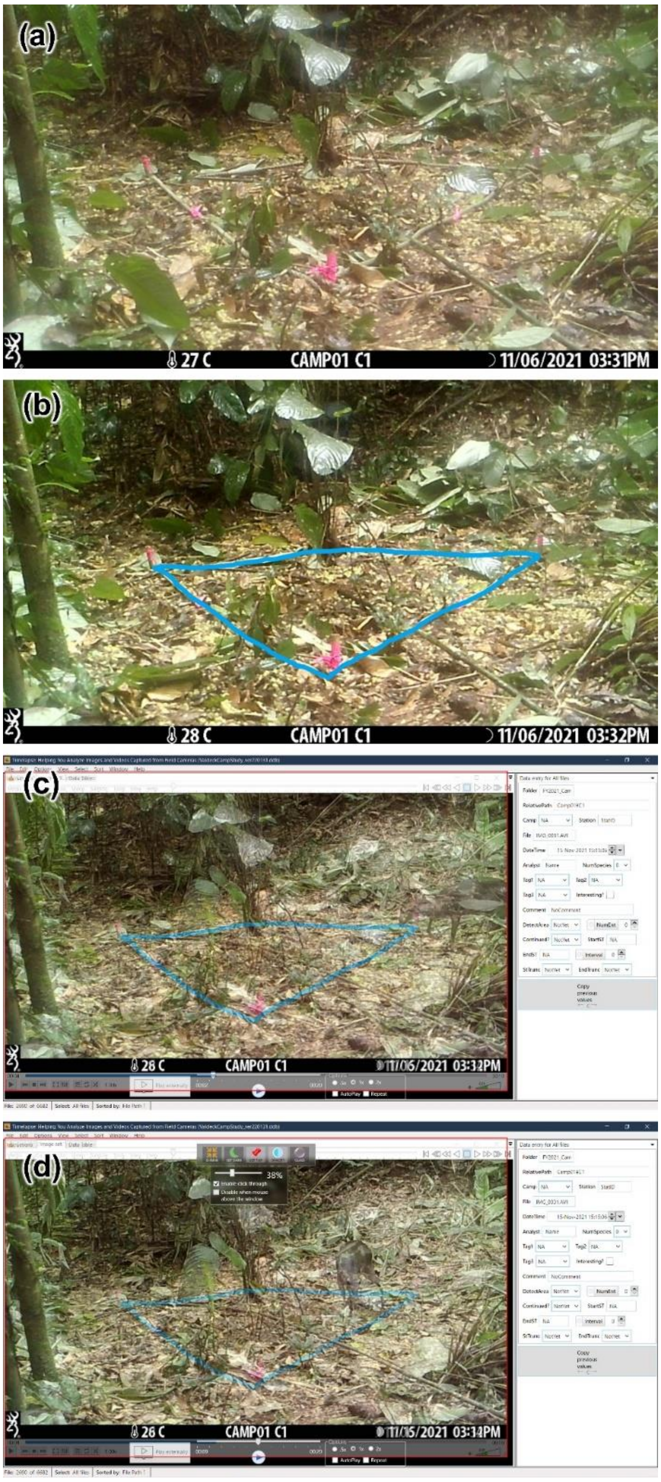

Fig. 6 Procedure for judging animal entries in the focal area and measuring their staying time. (a) A captured image of the focal area from the video recorded at the camera installation. (b) The same image with the focal-are rope traced in blue for highlighting. (c) The focal-area image opened with the VLC media player was transparentised using WindowTop and superimposed on the Timelapse window. (d) Transparency of the focal-area image was increased, and the video in Timelapse was played to judge the animal entry and measure the staying time.

Data shaping and cleaning

After processing images with Timelapse, the analysts export the data to a CSV file. But this CSV needs shaping to use in statistical modelling. Also, another CSV file for the data on camera working days. So the final product should be two CSV files in the formats shown in Fig. 7. Careful handling and error checks are required to avoid any mistakes in these files.

1. Data on passages

Station	Date	Time	Species	Stay	React	R_censor
CAM01	2022/02/14	17:32:43	b_duiker	4.6	0	0
CAM01	2022/02/16	08:22:59	b_duiker	0.3	1	0
CAM01	2022/02/19	12:56:01	b_duiker	6.1	0	1
CAM02	2022/02/21	18:00:04	b_duiker	2.4	0	1
CAM02	2022/02/28	15:38:41	b_duiker	1.8	0	0
CAM03	2022/02/25	07:07:34	b_duiker	9.1	0	0
CAM03	2022/03/01	14:56:22	b_duiker	4.4	0	0
...	...	...	...	...	...	...
...	...	...	...	...	...	...
...	...	...	...	...	...	...
...	...	...	...	...	...	...
CAM25	2022/02/28	08:09:15	b_duiker	1.5	1	0
CAM25	2022/03/10	17:34:41	b_duiker	7.1	0	1

2. Data on camera working days

Station	Days
CAM01	28
CAM02	41
CAM03	38
CAM04	45
CAM05	36
CAM06	45
CAM07	45
...	
...	
CAM24	33
CAM25	29

Fig. 7 Images of the two CSV data files required for statistical analysis using the REST model. The column "React" indicates whether the passed animal reacted to the camera (1) or not (0). The column "R_censor" represents whether the stay was right-censored (1) or not (0).

Statistical analysis to estimate density

After completing the data cleaning, analysts are ready to dive into statistical modelling—the most exciting but also the most bothering part of wildlife monitoring. To perform the REST modelling, the analysts need to acquire a certain level of knowledge and skills in statistics and programming languages. We often use a Bayesian approach to implement REST using **R** (R Core Team 2021) and **Stan** (Stan Development Team 2021), but the frequentist approach can also be acceptable if the model structure is simple. The analysts are strongly encouraged to refer carefully to previous study papers (Nakashima et al. 2018; Nakashima et al. 2020) and instructions in a preprint (Nakashima et al. 2021). We also provided example scripts to analyse the data and estimate density using REST with frequentist and Bayesian approaches in Supplementary Materials.

6. Perspectives

Estimating animal density is central in population ecology and wildlife management but is difficult to achieve, particularly in rainforests. Camera traps have the potential to overcome this challenge but need to be used with an appropriate method to get accurate estimates. This handbook 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 contents here can also be helpful when applying other models. The keys are to understand the formula and assumptions of the model correctly and to develop a monitoring plan accordingly.

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. So share and discuss your draft with your collaborators and colleagues, then revise the plan. Moreover, we hope more camera trappers share their monitoring plans in their articles and reports. If it’s impossible to include the detailed methods in a research paper, it may be shared on open access platforms, such as social networking sites like ResearchGate (https://www.researchgate.net/). These practised protocols will undoubtedly be helpful to others considering a new plan, as well as guaranteeing the reproducibility of your monitoring. We hope that this practical guide will help field managers to produce much more practical and sophisticated camera trap monitoring.

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Camera Trap Monitoring for Wildlife Density Estimation with the REST Model

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