The precision and accuracy of the Random Encounter and Staying Time Model's estimation of species population density

by

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ABSTRACT

1 *Introduction:* Species density is perhaps the most sought-after measurement in ecological research because it has a key role in conservation management practices and species monitoring. One method to measure density is to implement camera traps in ecological environments that takes continuous photographs at short time intervals to create a time-lapse, or records a video of animals throughout the night and day. Camera-trap data can be used to derive density estimates using the Random Encounter and Staying Time (REST) model for non-distinguishable individuals in a population.

2 *Methods:* I mathematically recreate the REST model under the theoretical framework of ideal gas law physics. I use this as a basis to derive the mean and variance of the REST model using probability density functions and mathematical moments. I use three different detection zone areas, research periods, and animal speeds to see how it affects the accuracy and precision of the density estimates.

3 *Results:* Assuming all assumptions of my model have been met, the REST model will give biased density estimates depending on the detection zone shape and the movement patterns of the species. The model's density estimates become more precise for longer research periods and larger detection zones. Faster moving animals also produce more precise density estimates. The mean estimate remains a true reflection of the species density regardless of camera detection zone, research period, or animal speed.

4 *Synthesis and application:* My work uses a combination of statistical distributions and mathematics to predict pre-emptively the precision and accuracy of the REST model without empirical data. This allows researchers to be able to change the REST model's parameters, research period and detection zone area, in accordance with the species movement speeds to

have an idea about the expected results the REST model will provide. Given that our work relies strictly on theoretically reasoning, we believe that this allows for our work to be applicable to a broad range of species, compared to if we had used empirical evidence. Given the popularity of the REST model, our work is anticipated to be very relevant to many future research monitoring projects.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 DENSITY BACKGROUND

Monitoring is the foremost practice upon which wildlife management depends. The number of animals within a given area – or species density – is of particular importance for species conservation and management practices. To successfully monitor density, methods should be accurate, where the estimated species density is unbiased to true species density, and precise, so that there is high certainty in the confidence of the estimates. Species density helps to determine the carrying capacity of habitats to be estimated, which in turn can be used to evaluate habitat productivity (Gaillard *et al.*, 2010). Furthermore, it allows researchers to understand the distribution of animals across a landscape. For example, species that are highly concentrated in one area face greater risk of extinction due to the lower number of localities (Staude, Navarro and Pereira, 2020). If that environment changes, animals must either acclimate, adapt, or they will be extirpated. Extirpations are often considered a prelude to species extinctions (Ceballos, García and Ehrlich, 2010). Currently, the world is facing its sixth Biodiversity Extinction Crises (Ceballos, García and Ehrlich, 2010) and hence there is a dire need to monitor populations of animals to help protect the biodiversity of the planet.

Camera traps provide an innovative way to monitor mobile species density. They have been gaining traction because they are non-invasive, comparatively inexpensive, and versatile in a variety of environments. Typically, camera traps use heat-sensitive infrared sensors to detect animals in front of the camera, in the detection zone. Once an animal is detected, the camera snaps a photograph of the individual using time-lapse photographs. Faster times between photographs yield higher sampling effort. Camera traps use white or infrared flash to capture animals during the night and can monitor species unattended 24 hours/day for months without maintenance. Higher quality cameras will have higher sensitivity, faster trigger time, longer battery life, and be more durable (Caravaggi *et al.*, 2017). One of the main issues that users face with camera trap monitoring is image classification (Glover-Kapfer, Soto-Navarro and Wearn, 2019). Camera traps have high rate of false positive detections (Newey *et al.*, 2015) and capture species that enter the detection zone regardless of their relevance to the study. The data must be sorted through using either trained technicians, computational software (Delisle *et al.*, 2021), or citizen science helpers (Glover-Kapfer, Soto-Navarro and Wearn, 2019). Theft and vandalism are other key issues that cameras face. The average price of a camera ranges from anything between $50 to $1000, however most mid-range cameras are suitable for species monitoring, costing approximately $300-$500 (Rovero *et al.*, 2013; LaFleur and Pebsworth, 2017). Managers often choose to buy less expensive cameras to maximize replication and spatial coverage assuming that they will perform adequately (Newey *et al.*, 2015). The diversity of species, topics, and ecoregions that camera traps are used for has been increasing steadily since 1995 (Delisle *et al.*, 2021).

Finding a way to use camera trap data for determining density of a species increases the versatility of cameras, however determining species density using camera trap data is complex. While the number of pictures can work as an index to show trends in the number of animals in the area over time, it does not estimate the number of individuals in an area since it does not consider animal movement patterns and detection probability. Indices are only useful as a proxy and consequently can only be used if estimating density is not necessary, which is rarely the case. For instance, for animals experiencing highly variable population dynamics or risk going extinct, accurate density estimates are necessary. The first analytical approach to come out that gave an estimate of true species density was the capture-recapture model (Karanth, 1995). Used many times in field experiments, the capture recapture model estimates density by identifying the reoccurrence of identifiable individuals within a resample episode. The ratio of the marked individuals at the resampled time represents the size of the population. With cameras, samples are taken over a time where individuals are captured within the camera detection zone. Of course, this only applies to species that have unique characteristics that identify the individuals for humans, such as coat colour or markings. This method has been used for tigers in Nagarahole National Park (Karanth, 1995) and bobcats in the southern California (Alonso *et al.*, 2015), however it is not a popular method due to the limited number of species it can be used for.

To date there are eight models in the literature that estimate species density and do not require individual recognition (reviewed in details below). The N-mixture model (Royle, 2004) was the first paper to come out, and due to its seniority, it has had the most exposure to various field tests in ecological environments. Shortly after, Rowcliffe *et al.* (2008) used a new approach, the Random Encounter Model (REM) to estimate density using ideal gas physics laws, however, it requires accurate measurements of animal speed and group size, parameters that are difficult to measure using camera traps. Nakashima Yoshihiro, Fukasawa Keita (2018) used similar methods as the REM to create the random encounter and staying time (REST) model that does not require animal speed or group size. In this way, they argue the model is more versatile and easy to apply to populations than it's precessor, the REM. At the same time as the REST was derived, Moeller, Lukacs and Horne (2018) derived three additional methods, each one a modification to the last: the time-to-event method; the space-to-event method; and the instantaneous sampling method. Similar to the REM, the time-to-event model requires animal speed to account for movement patterns that affect the time elapsed before an animal is detected in the camera detection zone.

The space-to-event model was created to eliminate this parameter by using space instead of time as it's measurement. The instantaneous sampling method uses the same the framework of the first two models to estimate density, however, can be used for a single moment in time. Two different methods, the distance sampling using camera traps method (Howe *et al.*, (2017) and spatial capture-recapture model (Chandler and Andrew Royle, 2013) use traditional methods already utilized with species in the field, however explain how to use camera traps instead of observers. The distance sampling using camera traps method states that a camera is considered an observer and the distance between the camera and the animal must be accurately measured. The unmarked spatial capture-recapture model is a modified version of the capture-recapture model.

1.2 SURVEY OF AVAILABLE MODELS THAT estimate DENSITY FROM CAMERA TRAPS

The N-mixture Model

The N-mixture model (Royle, 2004) is a model that uses spatially replicated count data at multiple surveys to obtain a density estimate for each camera trap. Assuming that an interaction between an animal and a camera can be considered an independent event, a Poisson distribution is used to model the encounter rate between an individual and a camera, and a binomial distribution is used to determine the probability of detection. There have been nine variations of the model that have emerged (see Dénes, Silveira and Beissinger, (2015) for an overview). The variations of the basic N-mixture model include the Royle-Nichols, zero-inflated, temporary emigration, beta-binomial, generalized open-population, spatially explicit, single visit and multispecies models. These variations incorporate detection error and variation in population size to make the N-mixture model more adaptable.

The N-mixture model assumes population closure, all individuals have an equal probability of being detection, that there are no false positive detections, detections remain independent at a camera throughout space and time, and that cameras are spaced far enough apart that the effective sampling area of a camera does not overlap other camera traps. Unlike many camera trap models, the N-mixture does not require random camera placement, and cameras can be baited to attract higher contact rates with the animals (Stewart, Volpe and Fisher, 2019).

One of the main draws of the N-mixture model is that is has been tested in a wide variety of ecological settings (Belant *et al.*, 2016; Shamoon, Saltz and Dayan, 2017). However, the N-mixture is sensitive to assumption violations. For instance, (Link *et al.* (2018) demonstrates that a 2% detection rate error can produce a bias that is greater than 20%.

Random Encounter Model

The random encounter model (REM) (Rowcliffe *et al.*, 2008) treats individuals like gas particles moving through space, using animal movement patterns to estimate the number of contacts that occur between an individual and a camera traps detection zone. The REM requires measurements of the camera detection radius and the horizontal angle of view, and an accurate estimate of animal speed and animal group size to be calculated (see Rowcliffe *et al.* (2008) for ways to do this). The REM estimates density within the sampling frame - the collective viewshed of the cameras.

The REM assumes random placement of the cameras, animals conform adequately to the ideal gas model used to describe the detection process, the detection zone is determined using appropriate methods, the population does not experience any immigration, emigration, births, or death during the study (closed population), and that animals move independently of the cameras. The REM has been criticized for having restrictive assumptions (see Foster and Harmsen (2012)), specifically having animals move randomly and independently from each other (ballistic movement) and having random camera placement. Rowcliffe *et al.* (2013) clarifies that these assumptions do not need to be met if animals move randomly with respect to the cameras. This means cameras must be placed in a way that is representative of the sampling study, without targeting or avoiding features in the landscape. Some sampling distributions that meet these criteria are random sampling, or stratified sampling distributions.

One of the main disadvantages to the REM is the number of additional parameters required for the model (but see (Rowcliffe *et al.*, 2016)). Specifically, estimating animal speed and group size can prove difficult to obtain without additional data collected, and incorrect parameterization impacts the accuracy of the density estimate (Cusack *et al.*, 2015). The REM is sensitive to inaccurate estimates of group size (Chauvenet *et al.*, 2017), animal speed (Manzo *et al.*, 2012), and non-random animal movement patterns with respect to camera traps (Cusack *et al.*, 2015). The REM has given imprecise density estimates in some ecological settings (Cusack *et al.*, 2015; Balestrieri *et al.*, 2016; Chauvenet *et al.*, 2017) and precise estimates in others (Rowcliffe *et al.*, 2008; Zero *et al.*, 2013; Caravaggi *et al.*, 2016; Schaus *et al.*, 2020). For instance, the REM was successfully used to estimate the European pine marten (Manzo *et al.*, 2012), the first application of the REM on a wild carnivore population, following the testing of the REM estimating three out of four species with known densities in an enclosed area correctly

(Rowcliffe *et al.*, 2008). When the REM does incorrectly estimate density, possible confounding variables could be animals not moving randomly throughout the environment (Cusack *et al.*, 2015) which could occur for very social species (Chauvenet *et al.*, 2017). The model estimates are optimized when the number of cameras deployed and the number of days is increased (Caravaggi *et al.*, 2016). Rowcliffe *et al.* (2008) recommends the research period be long enough to obtain at least 10 photographs and at least 20 camera locations should be deployed, with 40 being preferable. An extension has been developed for acoustic detectors (Lucas *et al.*, 2015) potentially broadening versatility of the model to species such as songbirds.

Time-To-Event Method, Space-To-Event Method, and Instantaneous Sampling Method

The time-to-event (TTE) method (Moeller, Lukacs and Horne, 2018) determines the amount of time prior to an individual being detected to calculate the rate of individuals in a given area. The model assumes animals rate of contact is Poisson distributed and the time between each interaction follows an exponential random distribution. The TTE method accounts for faster moving animals contacting the detection zone more frequently using animal speed to derive the length of the sampling period. In this way, higher contact rates for faster moving animals do not inflate density estimates.

The space-to-event (STE) method (Moeller, Lukacs and Horne, 2018) is an extension of the TTE method. The STE method uses space until first detection instead of the amount of time until first detection, as in the TTE method. It does this by setting all cameras to go off at continuous time intervals occurring simultaneously, where each trigger is considered a sampling period. The cameras are then checked at each sampling period until an individual is spotted. The order in which cameras are checked for each sampling period is randomized. In this way, rate of space use can be used to determine the rate of individuals in the area, or density of the species. This extension was derived to eliminate the requirement for animal speed, which is difficult to measure and has the potential to bias density results.

The instantaneous sampling (IS) method (Moeller, Lukacs and Horne, 2018) is a simplified version of the TTE method and the STE method. It uses a fixed area counts of animals captured on camera over the total research period and over the space use of all cameras to determine density. The cameras are set up to do repeated instantaneous triggers occurring at the same time over repeated intervals in the same manner as the STE method.

All three models work under the same four assumptions: random camera placement, population closure, independent observations of animals, and perfect detectability of animals. Due to the trigger rate following set intervals for the STE and IS methods, assuming perfect detection is realistic. However, the TTE method depends on perfect detection of all animals that cross the detection area. The STE and TTE methods have the additional assumption that animals contacting a camera follows a Poisson distribution. Moeller, Lukacs and Horne (2018) acknowledge that this assumption will not work in heterogenous environments where animals might clump due to landscape features.

Due to the three methods' novelty, none has yet been rigorously tested. Moeller, Lukacs and Horne (2018) found that the methods gave comparable density estimates to aerial surveys. Movement rate parameterization can compromise the overall density estimate for the TTE method (Loonam *et al.*, 2021). All methods require further testing for their applicability in various field settings.

Distance Sampling Using Camera Traps

Distance sampling using camera traps (CT-DS) (Howe *et al.*, 2017) uses the distance an animal is from the camera to obtain an estimate of density. The CT-DS method is a modification of traditional distance sampling (Buckland *et al.*, 1993), where an observer walks a predetermined area and counts the number of animals and the distance between themselves and the individual. Animals further away will have a decreased probability of detection. A detection function fits the frequency of occurrences which is then used to estimate density (Buckland *et al,*, 1993). The CT-DS method uses this framework but instead determines the frequency of snapshots of animals triggering the camera, and the area covered is the cumulative detection zones of the cameras (Howe *et al.*, 2017).

The CT-DS method assumes that animal's locations are independent of each other and the camera, that cameras are placed randomly, that animals at distance 0 are detected perfectly, animals are detected at their initial location prior to any movement and distance between the camera, population closure, and the individual is measured accurately. To meet the last criteria, one must measure each individual camera's view shield, the temporal sampling effort across all cameras, and the distance of each individual detected independently.

While distance sampling has been used extensively (Jathanna, Karanth and Johnsingh, 2003; Ruette, Stahl and Albaret, 2003), CT-DS is still considered a novel method. To date, CT-DS has been used for antelopes (Amin *et al.*, 2021), bharal and musk deer (Pal *et al.*, 2021), mountain hares (Bedson *et al.*, 2021), chimpanzees (Cappelle *et al.*, 2019), marmots (Corlatti *et al.*, 2020), and bighorn sheep (Harris *et al.*, 2020). The computational requirements are high for CT-DS (Thomas *et al.*, 2010), mainly because of the goodness-of-fit testing and model selection.

For this reason, the CT-DS might be best used for species of low abundance to reduce the time constraints and computational effort.

Unmarked Spatial Capture-Recapture Model

The unmarked spatial capture-recapture (USCR) model, also known as spatial count (SC) model (Chandler and Royle, 2013) uses the spatial correlation of animal movement patterns between traps to estimate the activity centers (loosely defined as the centroid of the the animal's home range, and can change based on the biology of the species) of the animals. The activity centers give the probability distribution of an individual being detected by a camera, where a scale parameter must be defined for the encounter rate of animal's detection probability decreasing with increasing distance from their activity centers. Density is thus defined as the number of activity centers divided by the area of the sampling regime.

The USCR assumes that the activity centers do not move, cameras do not attract or repel the animals, animals further from their activity centers will be spotted less frequently, and the sampling frame contains all activity centers. The model also assumes no false positive or negative photographs are taken. The model requires that cameras are spaced close enough together that individuals are spotted at multiple cameras. The USCR model may not be a viable choice for animals that do not exhibit territorial behaviours since animals are detected less frequently as the distance between the activity center and the camera increases and that the sampling frame contains all the activity centers of the animals detected by cameras. Further, due to the USCR requiring individuals to be spotted at multiple cameras, cryptic or low-density species might not meet this criterion.

One prevailing advantage is that the USCR has a clearly defined area, which is quantified as the area that includes all activity centers. However, the USCR is highly sensitive to the parameterization of the scale parameter (Sun, Fuller and Royle, 2014), and cameras must be placed strategically to accommodate all the assumptions. Lastly, the model is restrictive to Bayesian frameworks and is computationally expensive (Gilbert *et al.*, 2021). Generally, the USCR has not been used in many research studies (but see Sollmann *et al.* (2013)), has given imprecise results (Augustine *et al.*, 2019), and should be used with caution (Gilbert *et al.*, 2021).

Random Encounter and Staying Time Model

The random encounter and staying time (REST) model (Nakashima, Fukasawa, and Samejima 2018) is a novel model that is gaining traction due to its feasibility and utility (Gilbert *et al.*, 2021). Already, a variation of the REST model is being used by the Alberta Biodiversity monitoring institute (ABMI, 2020), and in multiple survey programs (Warbington and Boyce, 2020; Becker *et al.*, 2021; Laurent *et al.*, 2021). In simplistic terms, the model states that density will be equal to the cumulative time all the individuals within a species spend within a detection zone, divided by the observation period and the detection zone area (i.e., the sampling effort). The size of the detection zone area and the length of the observation period are determined by the researcher, and motion-triggered photos are used to measure the cumulative time of animals within the detection zone. The REST model is often considered a variation to the REM since the model was derived using similar assumptions about animal movement patterns (Gilbert *et al.*, 2021), however, it does not require the auxiliary parameters of animal speed and group size.

The model has all the same assumptions as the REM that were created from the ideal gas law (Rowcliffe *et al.*, 2008; Nakashima Yoshihiro, Fukasawa Keita, 2018). It assumes 1) perfect detection within the camera focal area 2) animal density remains constant (no immigration, emigration, births, or deaths) during the research study period 3) animals are neither attracted nor repelled by the camera traps 4) cameras are randomly placed with respect to species movement and 5) observations of individuals must be independent events. Further, it assumes 6) the cumulative staying time in the focal area must represent a good fit for the distribution that animal movements follow and 7) the observed cumulative time must follow a given parametric distribution. Some cameras have a delayed trigger period after an initial shot, which may violate assumption 1 (Nakashima, Yajima and Hongo, 2021). Further, camera trap placing should be carefully designed to meet assumption 4. For instance, camera trap placement should follow a stratified or random distribution (Rowcliffe *et al.*, 2013) and one should account for imperfect detection (Yajima and Nakashima, 2021), either by testing cameras beforehand and omitting pictures in which animals react to the camera (Nakashima, Yajima and Hongo, 2021).

The REST model works best for species in high abundance since the sampling effort must be high enough to represent animal distribution. Further, the REST model can be used to accommodate spatial variation of animals over environmental variation using covariates (Nakashima, Hongo and Akomo-Okoue, 2020). The REST model has provided consistent measures of density to estimate blue duikers compared to classic line surveys (Nakashima Yoshihiro, Fukasawa Keita, 2018). Further, the REST model gave an accurate, yet imprecise estimate of lynx density (Doran-myers, 2018). Nakashima, Fukasawa, and Samejima (2018) shows empirically and using simulations that increasing the duration of the study, the number of cameras, and the number of locations makes the density estimates more precise. At least 25 camera locations should be used, and empirical estimates of duikers becomes more precise at 20-day research periods. Garland (2019) expanded on this work to quantify how movement patterns affect the density estimates of the REST model. Long periods of inactivity produce less precise estimates than individuals that move constantly.

Despite its growing popularity, the math behind the REST model remains mostly unexplored. That it provides unbiased estimates was theoretically argued based on verbal arguments with no formal model (Nakashima, Fukasawa and Samejima (2018)). Furthermore, the expected variance of REST estimates is unknown, and users are left without any practical tools to anticipate the accuracy or the precision of their survey given their design. Understanding the REST model's accuracy and precision helps utilize the REST model to its full capabilities.

Thesis Objectives

My thesis chapter uses mathematics and statistics to derive the REST model. Currently, the REST model is derived using theoretical thought processes based on the rate of a population encountering a camera detection zone area. Theoretically, the expected number of contacts between two objects can be modelled based on their velocities (or simply speed, if the direction of travel is assumed randomly distributed and constant), their effective radii (the distance between the point objects at which contact occurs), the time span, and the density of objects. In our ecological setting, these correspond to the speed of the animals, the radius of the camera's detection zone, the time period over which the camera was active and ready to detect the animal, and the density of animals (the quantity we are trying to estimate) and cameras. Using these ideas, I derive a modified REST model that builds off of the work done by Nakashima, Fukasawa and Samejima (2018). In biological settings, animal speed, research period length, and detection zone size will vary depending on the ecological system being studied and the design set-up. These parameters influence the precision and accuracy of the REST model's density results by affecting the number of individuals entering a detection zone area. I use mathematical moments to derive the mean and variance of the REST model's density estimates using biologically realistic animal speeds (0.1 m/s, 1 m/s, 5m/s), detection zone radii (5m, 10 m, 15 m), and research periods (1 month, 3 months, 1 year). I then use the method of moments to find the 95% confidence intervals surrounding the mean density estimate. Precise results reduce the uncertainty surrounding the estimates and increases repeatability of the results over time. Accurate results can be replicated over spatiotemporal variation and consequently can be applied to a variety of terrestrial environments. This is, to my knowledge, the first paper that uses an interdisciplinary approach to derive the REST model and find the precision and accuracy of the REST model from mathematics.

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CHAPTER 2: RECONSTRUCTING THE RANDOM ENCOUNTER AND STAYING TIME MODEL TO FIND THE MEAN AND VARIANCE OF SPECIES DENSITY

2.1 INTRODUCTION

Precise and accurate population density estimates are integral for management practices; however, estimating population density of mobile species has been a long-standing challenge in wildlife ecology and management. While measuring density appears to be straightforward, tracking spatial and temporal changes is usually constrained by the amount of time (Palomares 2001), money (Tear et al. 2005; Wilhere 2008), and labour efforts that are available (Hein 1997). Although traditional methods sometimes provide robust estimates (e.g. aerial surveys, quadrat and transect methods, mark-recapture sampling, distance sampling; (Hone 1988; Robson and Regier 1964), recent research advancements have used probability and likelihood functions to estimate density using camera trapping data. Cameras were initially being used as a way to measure species occupancy (presence/absence) data (Galvez et al. 2016) and to a lesser extent animal behaviour (Caravaggi et al. 2017). Cameras have become popular with agencies and researchers (Caravaggi et al. 2017; Moeller, Lukacs, and Horne 2018; Royle 2004; Chandler and Royle 2013; Rowcliffe et al. 2008; Nakashima Yoshihiro, Fukasawa Keita 2018; Howe et al. 2017). Camera traps' ability to monitor species over different landscapes is advantageous in situations where species are cryptic or in remote locations (Carbone et al. 2001), the species is small, (Villette et al. 2016) or when evaluating population changes over time (Caravaggi et al. 2017). Additionally providing density estimates broadens the camera traps' applicability and makes it a useful alternative monitoring tool for large-animal research practices.

Nine working models currently are in use applying camera trap data to estimate density (Howe et al. 2017; Nakashima, Fukasawa, and Samejima 2018; Rowcliffe et al. 2008; Chandler and Royle 2013; Royle 2004; Moeller, Lukacs, and Horne 2018; Burton et al. 2015; Karanth 1995). Within these, eight models do not require individual recognition (Table 1). For example, the Random Encounter and Staying Time (REST), proposed by Nakashima, Fukasawa, and Samejima (2018), estimates density using the likelihood of an individual entering a camera detection zone area based on its movement rates and the camera's viewshed. Despite the model's novelty, the REST model has been used to study multiple species, including blue duikers, sitatunga (Warbington and Boyce 2020), moose (Becker et al. 2021), and white-tailed deer (Laurent et al. 2021) and is expected to gain popularity quickly due to its feasibility and utility (Gilbert *et al.*, 2021). The REST model assumes that (1) cameras are placed randomly with respect to the spatial distribution of animals (2) cameras have perfect detection of animals within the focal area (3) population closure of the study period (4) animal movement and behaviour are not affected by camera traps (5) observations are independent events. Two protocols (Nakashima, Yajima, and Hongo 2021; Hongo, Nakashima, and Yajima 2021) have been developed that address these assumptions and proper procedures to follow to obtain the best density estimates for a population. Further, Nakashima, Hongo, and Akomo-Okoue (2020) extended the model to incorporate environmental covariates to estimate habitat-density relationships. The REST model has been shown to give accurate and precise results in most instances (Garland 2019; Doran-myers 2018), showing the REST model to have promise to be a functional and easily applicable model.

The theoretical framework, (modified from Nakashima, Fukasawa, and Samejima (2018)) states that, given a population of density ρ, the instantaneous expected number of individuals within a camera's detection zone a can simply be written as $\rho \cdot a$. If the research period T is sufficiently long, then the product, $\rho \cdot a \cdot T$, is equal to the cumulative time a species spends in front of the camera $\sum t_i$ (where i indexes an encounter event between a camera and an individual). Rearranging for ρ, it is seen that density can be expressed as a function of time an animal spends in front of the detection zone, the size of the detection zone, and research time.

$$\rho = \frac{\sum t_i}{T \cdot a}$$

The REST model builds upon its predecessor, the Random Encounter Model (REM). REM applies a similar framework, where individuals move autonomously throughout an environment, independent of camera placements and conspecifics. Although the two models work under similar assumptions, the REM requires approximations for the average daily movement rates for a species (Rowcliffe et al. 2008). The REST model instead uses cumulative time an animal spends in front of a detection zone, an easily measurable and therefore more ecologically functional parameter.

Nakashima, Fukasawa, and Samejima (2018) created a density model grounded on theoretical reasoning and logic. We show REST is consistent with a mathematical model grounded on ideal gas law physics. We then use our model to derive the expected variance of the REST-density estimates. We thus provide theoretical limits on the usefulness of REST estimates, given the sampling effort.

2.2 METHODS

The REST model relies on an empirical measure of the cumulative time an animal spends inside of a detection zone, $\sum t_i$. Note that $\sum t_i = n \cdot E(t)$ where n is the number of encounters between a species and a detection zone and $E(t)$ is the average time individuals spend within the detection zone. The derivations of each separate part of this simple equation provide a straightforward way to recreate the REST model mathematically.

Statistical moments for the time it will take an individual to travel through the detection zone

Imagine an animal travelling along a straight trajectory in which it traverses a circular camera field of view at a constant speed, *s*. Note that we are assuming the field of view is circular here for mathematical simplicity (we shall review this assumption in chapter three). As the animal's heading is random relative to the camera, it may enter the field of view at any angle between 0 and π (see Fig. 1 for more details, note that due to symmetry, the circle is cut in half, however it does not affect the final answer). The time spent traveling through the camera's field of view, *t*, is a random variable of the uniformly distributed angle of entry, θ, and can be expressed as

$$t = \frac{2 \cdot r \cdot cos\ (\theta)}{s} \tag{1}$$

where r is the radius of the detection zone. The cumulative distribution function of time t is Eq. 1, rearranged for the probability of an angle θ being below or equal to a time t of the animal and a radius r of the camera detection zone,

$$F_T(t) = 1 - \left[\frac{2}{\pi} \cdot cos^{-1}\left(\frac{s \cdot t}{2 \cdot r}\right)\right] \tag{2}$$

is used to determine the probability of a random value being less than or equal to a random value in question. Probability density functions are the derivative of the cumulative density function. They describe the probability of a continuous value falling within a range of values. The probability density function for time spent inside the detection zone can be written as:

$$f_T(t) = \frac{2}{\pi} \cdot \frac{s}{\sqrt{(2 \cdot r)^2 - (t \cdot s)^2}} \tag{3}$$

Probability functions have the further use in that they are a simple way to find a function's moments (see appendix 1 for the structure of raw and central moments). Moments are, in essence, a way to characterise a distribution of a random variable. The first moment gives the mean of the function and the second moment gives the variance of the function (higher moments, not derived in this paper, are the skewness and kurtosis).

The first moment, the average time an animal is expected to spend inside the camera detection zone, $E(t)$, is calculated as the PDF, $f_t(t)$ (Eq. 3), multiplied by t, and integrated over all possible values for t. In other words, the mean of the distribution is given by a weighted average of all possible values, where weights are given by the probability of each value occurring under this distribution. The resulting integral is bounded between 0 (given that time exists on a positive continuum) and $\frac{2r}{s}$ (as seen in Fig. 2).

$$E(t) = \int_0^{\frac{2 \cdot r}{s}} \frac{2}{\pi} \cdot \frac{s}{\sqrt{(2 \cdot r)^2 - (t \cdot s)^2}} dt = \frac{4 \cdot r}{\pi \cdot s} \tag{4}$$

The second raw moment is calculated using similar methods, except that t is transformed to t^2 within the integral. Raw moments are considered standard for the mean (first moment), however second moments are central by nature. The variance is thus adjusted about the mean by subtracting the first moment squared $(\frac{4r}{\pi s})^2$ from the integrated second raw moment,

$$E[t^2] = \int_0^{\frac{2\cdot r}{s}} \frac{2}{\pi} \cdot \frac{s^2}{\sqrt{(2\cdot r)^2-(t\cdot s)^2}} dt = \frac{\mathbf{2}\cdot r^2}{s^2} \qquad (5)$$

$$Var[t] = E[t^2] - E[t]^2 = \frac{\mathbf{2}\cdot r^2}{s^2} - \left(\frac{4\cdot r}{\pi\cdot s}\right)^2 \qquad (6)$$

We see that the mean, $E(t)$, and variance, $Var(t)$, are both functions of the ratio between the radius of the detection zone (the square root of the effective area) and speed of the animal, where a larger radius increases the parameter's values and the faster the individuals move through the camera view decreases both parameter's values.

Moments for the number of encounters between individuals and a detection zone

The ideal-gas law is used by physicists to describe the rate of collisions between gas particles moving at constant random velocities. It has been adapted by biologists to model predator-prey dynamics (Vander Vennen et al. 2016), fertilization kinetics (Randerson and Hurst, 2001), and movement patterns (Rowcliffe *et al.*, 2008). The ideal-gas law assumes that gas particles move in a random yet constant direction and speed (coined 'ballistic movement' in ecology) in a confined space (so that particle density is constant), large enough to make any boundary effects (collisions with the walls of the domain) negligible. Under these assumptions, the expected number of encounters between a focal gas particle (or random point in space) and all other gas particles, n, is equal to the area of travel, the product of the length of the particle $2 \cdot r$ by the distance it traverses, multiplied by the density of particles ρ. Distance is the speed of the particle s multiplied by time T,

$$n = 2 \cdot r \cdot T \cdot s \cdot \rho \quad (7)$$

In an ecological setting, n is the number of encounters between individual animals and a circular detection zone with radius r, s is the speed of the animal, T is the research period, and ρ is the density of animals.

The Poisson point process is used for determining the probability distribution of a specified number of encounters n an animal has with a detection zone within the research period T. Poisson distributions are appropriate when events are discrete, independent, and the encounter rate is constant. The Poisson point process's PMF,

$$P(K = k) = \frac{\lambda^{k} \cdot e^{-\lambda}}{k!} \quad (8)$$

describes the probability of observing k events in a set time frame given that expected value (also called the 'Poisson intensity') is λ. In this case, λ is given by Eq. 7, the expected number of encounters between ballistically travelling animals and a single camera detection zone.

The first and second moments of a Poisson PMF are given by λ:

$$E(n) = Var(n) = \lambda = 2 \cdot r \cdot T \cdot s \cdot \rho \quad (9)$$

Notably, since both parameters are identical, the mean and variance are influenced by the same ecological factors and change at the same rate over time.

Statistical moments for the expected density

As long as the probability of an encounter is independent of the movement direction (and hence the time spent crossing the detection zone), the expected time animals spend inside a single camera's detection zone is modelled as $E(\sum t_i) = E(n) \cdot E(t)$. Using Eq. 4 and Eq. 9 above for $E(n)$ and $E(t)$,

$$E(\sum t_i) = (2 \cdot r \cdot T \cdot s \cdot \rho) \cdot \left(\frac{4 \cdot r}{\pi \cdot s}\right) = \frac{8 \cdot r^2 \cdot T \cdot \rho}{\pi} = \frac{8 \cdot a \cdot T \cdot \rho}{\pi^2} \tag{10}$$

where a is the area of the circular detection zone ($a = \pi \cdot r^2$).

Rearanging Eq. 10 we obtain the strutural backbone of the REST model, demonstrating that the mean time spent inside a detection zone, $E(\sum t_i)$, is a consistent estimator of animal density, ρ:

$$\rho = \frac{E(\sum t_i)}{T \cdot a} \cdot \frac{\pi^2}{8} \tag{11}$$

In other words, if T and a are known, and the model's assumptions are not violated, knowledge of $E(\sum t_i)$ is equivalent to knowledge of ρ.

Following product distribution laws of the two independent random variables n and t, the variance of the cumulative time a species is within a detection zone $Var(\sum t_i)$ (appendix 1):

$$Var(\sum t_i) = \left(\left(\frac{4 \cdot r}{\pi \cdot s}\right)^2 \cdot 2 \cdot r \cdot T \cdot s \cdot \rho\right) + \left((2 \cdot r \cdot T \cdot s \cdot \rho)^2 \cdot \left(\frac{2 \cdot r^2}{s^2} - \left(\frac{4 \cdot r}{\pi \cdot s}\right)^2\right)\right) +$$
$$\left(\left(\frac{2 \cdot r^2}{s^2} - \left(\frac{4 \cdot r}{\pi \cdot s}\right)^2\right) \cdot 2 \cdot r \cdot T \cdot s \cdot \rho\right) = \frac{4 \cdot \rho \cdot r^3 \cdot T(2 \cdot (\pi^2 - 8) \cdot \rho \cdot r \cdot s \cdot T + \pi^2)}{\pi^2 \cdot s} \tag{12}$$

Substituting $Var(\sum t_i)$ into the REST model, the variance for the density measurements $Var(\rho)$ simplifies to:

$$Var(\rho) = \frac{\frac{4 \cdot \rho \cdot r^3 \cdot T(2 \cdot (\pi^2 - 8) \cdot \rho \cdot r \cdot s \cdot T + \pi^2)}{\pi^2 \cdot s}}{T^2 \cdot a^2} \cdot \frac{\pi^2}{8} \tag{13}$$

To our knowledge, Eq. 13 is the first analytical approximation of the expected variation in density estimates under the REST model. We will later use it to demonstrate the usefulness of the model under different sampling scenarios.

Deriving the REST model: Part II

Above, we derived the REST model by envisioning the time it would take an animal to cross a camera trap given the size of the camera trap's detection zone, the trajectory of the animal, and the animal's speed. We can recreate the same equation using the same ideal gas law principles as before, however without determining distance an animal moves within the detection zone area or number of contacts between a population and the detection zone area. Despite these differences, we obtain the same mathematical expression.

Density of a species, using the ideal-gas law (Eq. 7, rearranged), is modelled as the encounters between a species and a detection zone per: radius of the detection zone, research period, and speed of the animal.

$$\rho = \frac{n}{2 \cdot r \cdot T \cdot s} \tag{14}$$

Although the ideal gas law's density measurement uses parameters that the REST model does not, the two models are, in fact, synonymous to each other. Here, we will derive the REST model in a second way and further recall the same REST model (Eq. 11).

Changing speed into the average distance an individual moves in the detection zone $E(d)$ per the average time a species spends in front of a detection zone $E(t)$:

$$\rho = \frac{n}{2 \cdot r \cdot T \cdot \left(\frac{E(d)}{E(t)}\right)} = \frac{n \cdot E(t)}{2 \cdot r \cdot T \cdot E(d)} \tag{15}$$

Further changing cumulative time $\sum t_i = n \cdot E(t)$ and radius into area, $a_{circle} = \pi \cdot r^2$,

$$\rho = \frac{\sum t_i \cdot \pi \cdot r}{2 \cdot a \cdot T \cdot E(d)} \tag{16}$$

The simple relationship, $distance = time \times speed$ solves for the average distance $E(d)$, where average time is derived as $E(d) = E(t) \cdot s$, ($E(t)$ derived in Eq. 4)

$$E(d) = \frac{4 \cdot r}{\pi \cdot s} \cdot s = \frac{4 \cdot r}{\pi} \tag{17}$$

The equation is recreated as

$$\rho = \frac{\sum t_i \cdot \pi \cdot r}{2 \cdot a \cdot T \cdot \left(\frac{4 \cdot r}{\pi}\right)} = \frac{\sum t_i}{T \cdot a} \cdot \frac{\pi^2}{8} \tag{18}$$

The REST model eliminates variables that are difficult to measure, such as the speed of the animal s and number of encounters an animal has with a detection zone n.

Visualising the results

Using the method of moments, we fit our derived mean from equation 11 and variance from equation 13 to the log-normal, Weibull, and gamma distributions to determine the 95% confidence intervals for the estimates (see appendix 3). The distributions were appropriate given that they all meet the criteria of being positive, continuous distributions. We compute these confidence intervals nine times, where, for each graph, we choose different biologically relevant research periods (one month, three months, and one year) and camera detection zone radii (five meters, ten meters, and fifteen meters) for an animal speed of 0.1 m/s (Table 2). We repeat his process for an animal speed of 1 m/s (Table 3) and 5 m/s (Table 4). The distributions give comparable results (appendix 4), and we focus on the log-normal distribution for our result analysis.

Density is a crucial parameter for species conservation and management practices. While the REST model by itself has been used to estimate density, deriving the mean, variance, and confidence intervals allows the researchers to determine the certainty and repeatability of the estimates. The mean, being always equal to the true density, shows consistency in the REST models estimates. The 95% confidence intervals, created using the variance derivation, show the certainty of the density estimates.

2.3 RESULTS

We derived two different sets of equations for a density estimate of the REST model using two different methods. We then created confidence intervals that show the precision and accuracy of the REST model's density estimates using an explicitly stated detection zone area to derive the staying time of an individual in front of a camera. In our second derivation, we used detection zone area to determine the contact rate between an individual and camera traps. The incorporation of detection zone area into our methods results in a modified REST model equation estimates density $\frac{\pi^2}{8}$ times greater (equation 18) than the model created by Nakashima, Fukasawa, and Samejima (2018). In other words, our derivation indicates that the ratio $\frac{\sum t_i}{T \cdot a}$ should provide a consistently biased (by a factor of ~1.23) estimate of density.

As the density of the species increases, the margin of error around the mean also increases, broadening the confidence intervals. The variables 1) research period and 2) detection zone radius (both under the control of the researcher) have different effects on the certainty of the estimates for species at high densities compared to the species that exist at low densities. For rare species, lengthening the research period and creating a large detection zone (e.g., by placing more cameras) improves the accuracy of the estimate (reduces the confidence intervals). In these cases, the confidence intervals tend towards a normal distribution about the mean and the upper and lower bounds become narrower. For short research periods and small detection zones, the confidence intervals are skewed above the mean such that there is a larger range of values that overestimate density with 95% certainty. When species density is high, changing the research period and detection zone does not influence the confidence range.

The animals speed also influences the confidence range. At low densities, the faster the speed of the animal, the more accurate the density estimates. Like research period and detection zone area, at high densities, the speed's effect on the size of the confidence intervals is negligible. Note that the speed does not influence the mean density estimate, which will always be equal to the true density of the species.

2.4 DISCUSSION

We showed that the REST model produces animal density estimates that are unbiased to true animal density. Our derivation shows that it is important to take the shape of the detection zone area into account, which the traditional REST model by Nakashima, Fukasawa, and Samejima (2018) does not account for. In this way, our estimates will estimate density to be $\frac{\pi}{8}$ times higher than the traditional density model. The precision of the estimates varies with species speed, camera trap detection zone area and research period. While animal speed is typically outside of the observer's control, camera detection zone area and research period can be manipulated to produce more precise density estimates. In fact, one simple approach to increase both a and T is to add more cameras. If the cameras can be reasonably considered independent, the larger the number of cameras, the larger the area that is being observed, and hence the higher the precision of the estimates will be. In homogenized environments, the summation of all independent camera trap's detection zone areas and research periods gives a density estimate for the entire sampling area.

The mean density is an unbiased estimator of the species true population density. Unbiased estimators work regardless of the spatiotemporal variation throughout the study site or the sampling equipment used (Carstensen and Lindegarth 2016), and consequently the REST model can be applied to a variety of terrestrial environments. While often sought after, unbiased results are not always necessary; indices such as number of photographs taken can be used as proxies to monitor changes in population abundance (Bengsen et al. 2011; Foster and Harmsen 2012; Palmer et al. 2018), where the relationship between number of photographs and animal density is oftentimes biased, and non-linear (Gibbs 1999). Comparatively, camera trap density models are often assumed to produce unbiased estimates of true animal density, due to the models accounting for the system's behaviour. Our findings are further supported by other studies; while the REST model is still new, it has been shown to produce unbiased density estimates when: used in simulations (Nakashima, Fukasawa, and Samejima 2018), controlled human trials (Garland 2019), and produces similar estimations of density as the spatial mark-resight (SMR) and spatial-capture-mark-resight (SCMR) models in field studies where the true species density remains unknown (Doran-myers 2018). While capture-recapture and spatial capture-recapture methods are most commonly used to estimate density from camera traps (CR – 54.8%, SCR – 33% of camera trap studies) (Burton et al. 2015), the methods have been known to produce biased results (Foster and Harmsen 2012). Due to its unbiasedness, we expect the REST model to end up being used more frequently, especially when obtaining unbiased density estimates is crucial, such as with endangered or low-density species.

Animal speed, research period, and detection zone area influenced the precision of our derived REST model density. Faster moving animals produced more precise results. Similarly, lengthening the research period or enlarging the detection zone area yielded precise density estimates. Precision is always desired in field studies; it reduces the uncertainty surrounding the estimates and increases repeatability of the results over time (Hellmann and Fowler 1999). While high-end camera traps are able to take up to 50,000 pictures without maintenance and capture photographs up to 30 m away from the lens under optimal conditions (Reconyk 2013), using these as research periods and detection zone areas are impractical. To meet the assumptions of perfect detection, a smaller detection zone area should be used (Rowcliffe et al. 2008), and shorter time periods could be used to meet the assumption of population closure (such that there is assumed to be no births, deaths, immigration or emigration within the research period time frame (Tobler and Powell 2013)). Further, there might be cost and labour restrictions that need to be accounted for (Palomares 2001; Hein 1997). While the most common research period for camera trap density studies is 8 months (n = 211), it varies considerably (between <a month to over 13 years), and oftentimes was left unspecified (Burton et al. 2015). Given that the design of the study has such an influence on the REST model precision, we recommend that researchers remain transparent and detailed about their designs. Each study system will have to find a balance between reducing the uncertainty of the estimates and accounting for the functional and theoretical limitations of the camera-trap REST model.

Under our mathematical assumptions, the REST model precision will only be influenced by research period, detection zone area and animal speed. However, animals do not behave like gas particles, and consequently the assumption of ballistic movement will be violated. While Rowcliffe et al. (2013) provides insight about how animals only need to move randomly and independently from the camera traps to not *bias* the results – proven mathematically (Hutchinson and Waser 2007) and in field studies (Rowcliffe et al. 2008) – non-ballistic movement has been proven to produce less *precise* results for the REST model in controlled human trials (Garland 2019). In field studies, the REST model produces the least precise results when compared to other models such as the REM, Formozov-Malyshev-Perelishin Formula, spatially explicit capture-recapture, spatial capture-mark-resight, and spatial mark-resight (Garland 2019). Consequently, for long-term monitoring programs, the REST model should be used with caution, and only for systems that consider the REST model's limitations.

Despite the shortcoming of ballistic movement our methods pre-emptively showed the level of uncertainty of the estimates, compared to ad hoc methods of measuring uncertainty used for most camera trap models. Further, they demonstrated under which systems and experimental set up the model will work best. As such, our results give insight as to which circumstances the REST model should be used for accurate, precise density estimates. For instance, the REST model gave low levels of variability compared to transect line surveys when measuring blue duikers (Nakashima, Fukasawa, and Samejima 2018) and, further, gives the lowest variability when at high sampling efforts (Garland 2019). Given that the REST model's estimates are unbiased, we argue that the REST model could be a superior model to other current working models under the right circumstances, however further research should be done before the REST model is used broadly.

Our paper has shown that the REST model can be used as an unbiased estimator for population density. The mathematical equations we derived reiterates the work done by

Nakashima, making the REST model an appealing model as it allows ecologists to be confident in its ability to measure species density. Further, we have outlined the situations in which the model should be used, given the anticipated variance around the mean density estimate. The REST model's ability to provide unbiased density estimates depends on the parameters of the model: researcher period, camera detection zone, and animal speed. If used correctly, the REST model could become a competitive method to estimate animal density, which is essential for animal conservation and management strategies.

763 ***Table 3***- A comparative chart of the assumptions and requirements of the eight working models that use camera trap data to

764 determine density, without the need for individual detection of the animals. The models are as follows: the spatial count (SC)

765 model, random encounter and staying time (REST) model, random encounter model (REM), N-mixture (N-mix) model, distance

766 sampling (DS) model, time-to-event (TTE) model, space-to-event (STE) model, and instantaneous sampling (IS) model.

	Requirements						Assumptions						
Model	**Sampling effort**	**Count or time data**	**Locations of detectors**	**Movement rate**	**Home range size**	**Area sampled by detector**	**Demographic and geographic closure**	**Random detector placement**	**Can use each camera independently to get estimates**	**No behavioural response to detector**	**Independent detections**	**Stable activity centers**	**Perfect detection within detection zone**
SC	Yes	Yes	-	-	Yes		Yes	Yes	-	Yes	-	Yes	Yes
REST	Yes	Yes	-	-	-	Yes	Yes	Yes	Yes	Yes	-	-	Yes
REM	Yes	Yes	-	Yes	-	Yes	Yes	Yes	Yes	Yes	-	-	Yes
N-mix	Yes	Yes	-	-	-	-	Yes	Yes	-	Yes	-		-
DS	Yes	Yes	-	-	-	Yes	Yes	Yes	Yes	Yes	-	-	-
TTE	Yes	Yes	-	Yes	-	Yes	Yes	Yes	-	Yes	Yes	-	Yes
STE	-	-	-	-	-	Yes	Yes	Yes	-	Yes	Yes	-	Yes
IS	Yes	Yes	-	-	-	Yes	Yes	YEs	-	Yes	Yes	-	Yes

Table 2 – 95% confidence intervals using the log-normal distribution of the expected range for the density estimates to fall, with the middle line being the mean estimate of density (which is the same as true density). These estimates were derived for one month, three months, and one year at three different radius sizes at the speed of 0.1 m/s

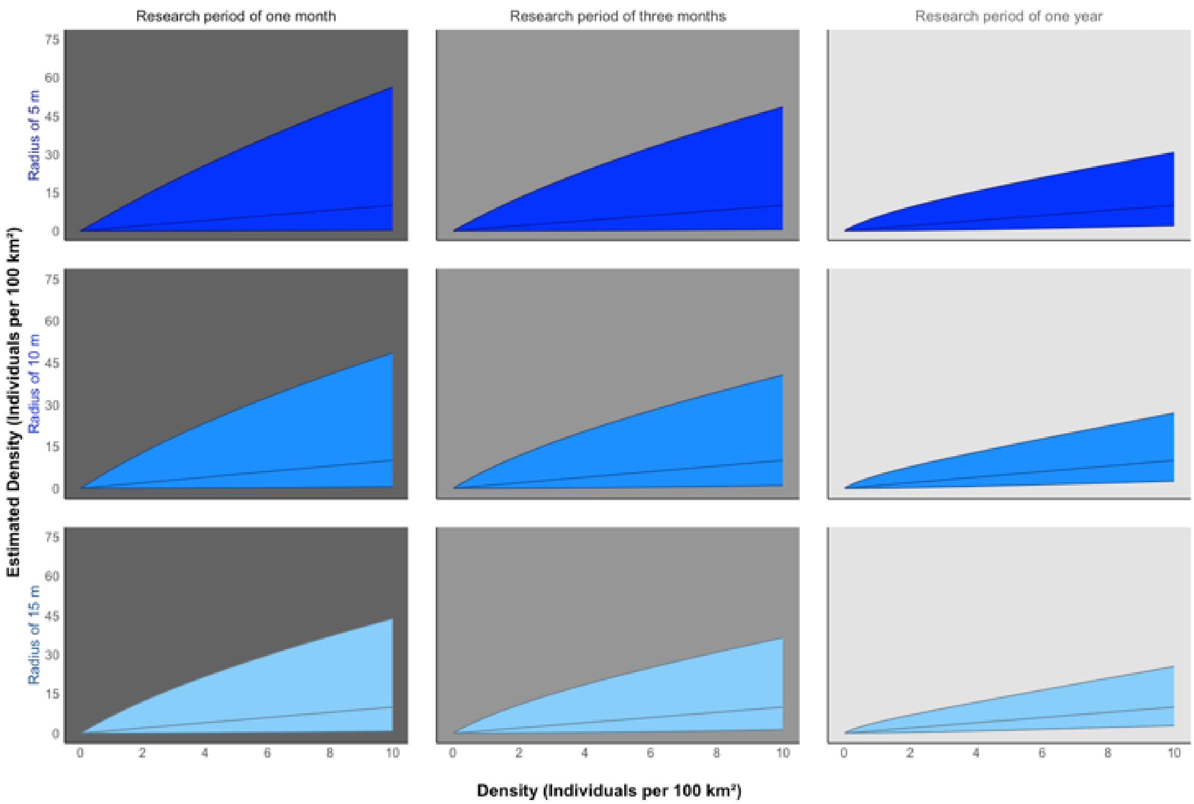


Table 3 – 95% confidence intervals using the log-normal distribution of the expected range for the density estimates to fall, with the middle line being the mean estimate of density (which is the same as true density). These estimates were derived for one month, three months, and one year at three different radius sizes at the speed of 1 m/s

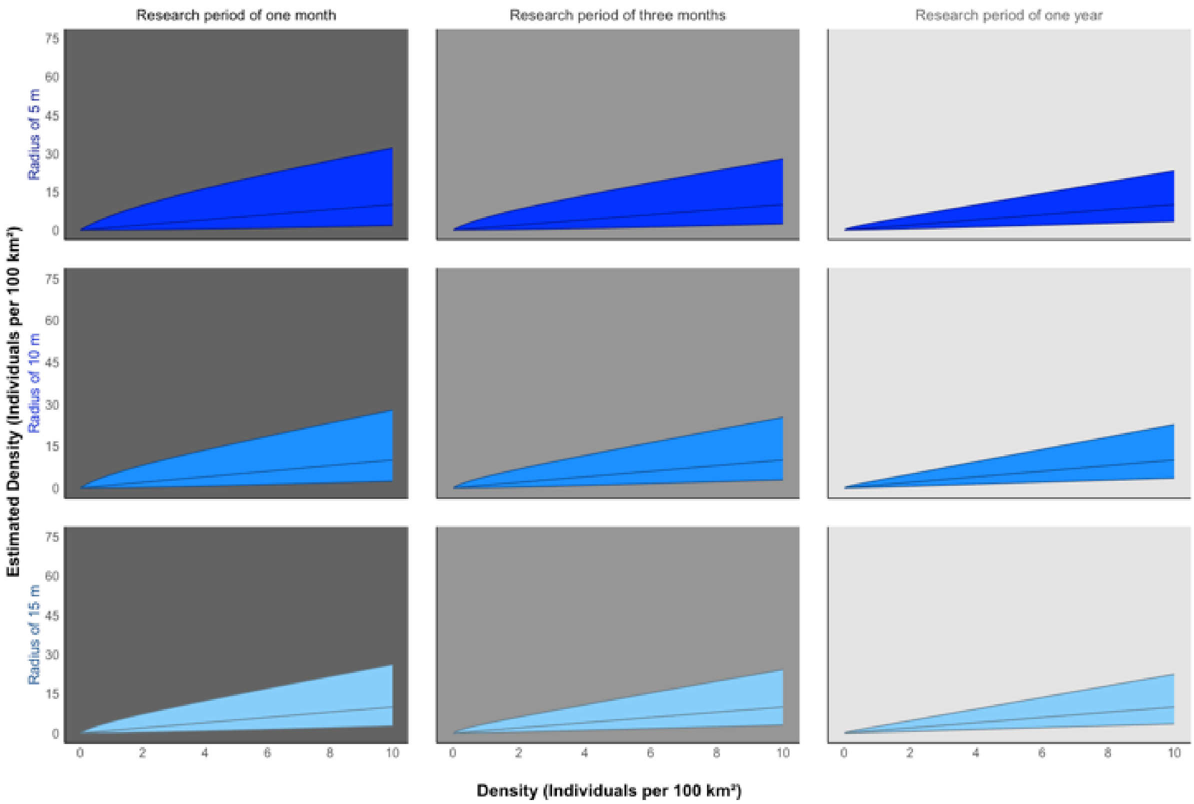
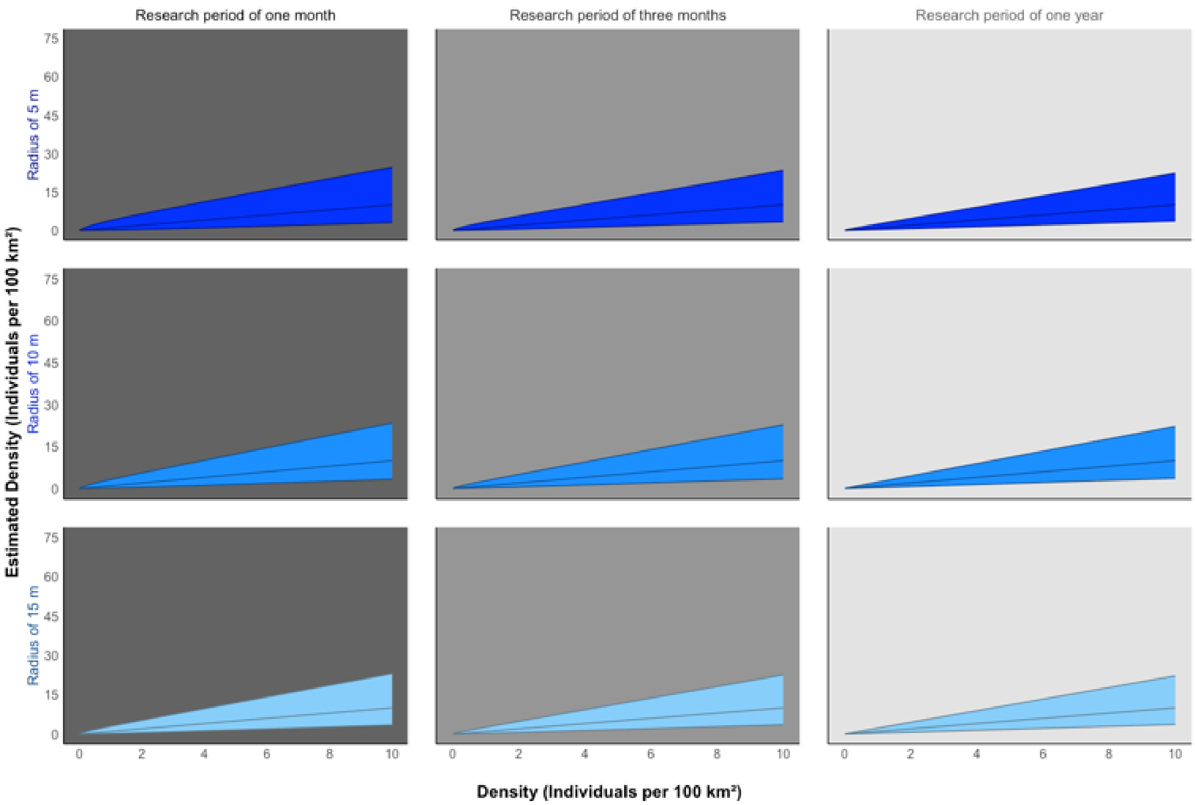


Table 4 – 95% confidence intervals using the log-normal distribution of the expected range for the density estimates to fall, with the middle line being the mean estimate of density (which is the same as true density). These estimates were derived for one month, three months, and one year at three different radius sizes at the speed of 5 m/s



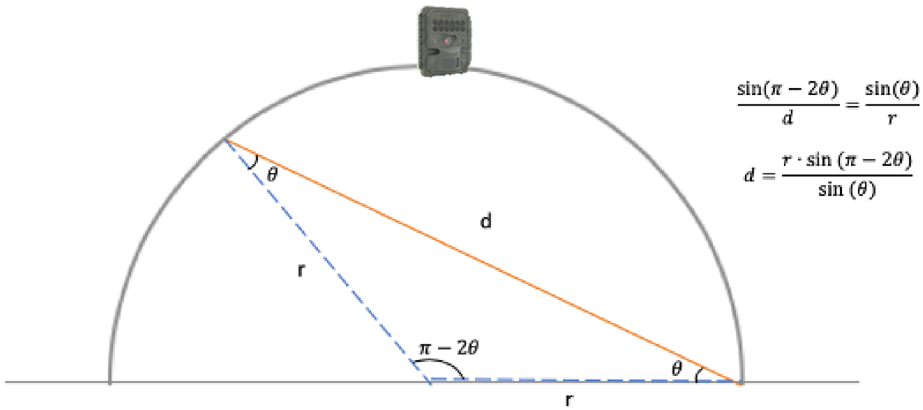


Figure 2 – Derivation of equation 3 and schematic figure showing theoretical framework of the camera trap. A camera is facing forward around a detection zone area (grey line). An animal enters the detection zone area at angle θ, travels distance d (orange line) and exits the detection zone. The detection zone is made to be circular for the derivations of the REST model, however, since a circle is symmetrical, choosing any line crossing a semi-circle and using the sine law gives the distance travelled across the circle. The derivations of the distance d the animal travels use sin laws to solve.

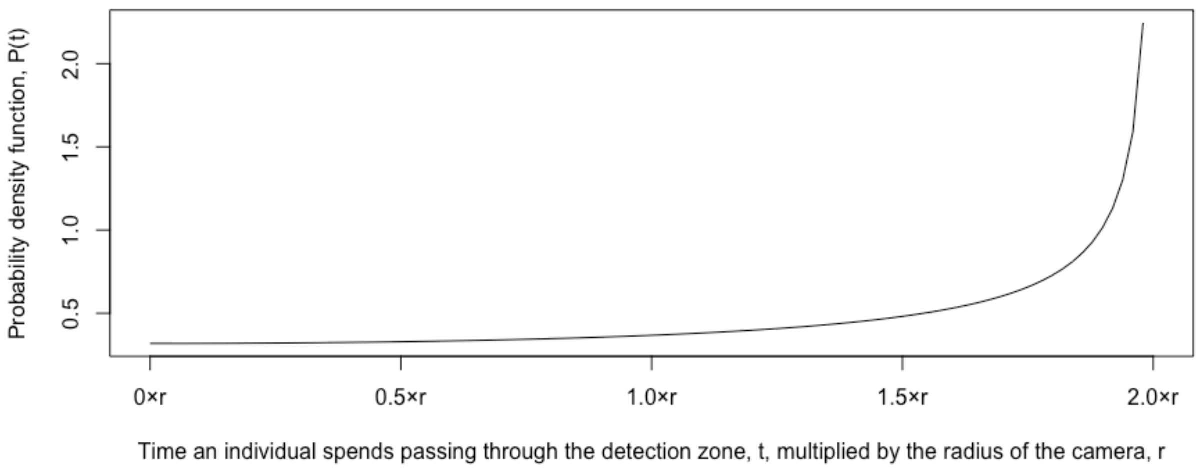


Figure 2 – Probability density function of the time that an individual spends within the detection zone, given that the radius r is set at a specified value. The time an individual spends is distance travelled divided by speed of the animal, and in this graph increases at an interval of 0.5 from 0 to 2. As seen, the indefinite integral is bound between 0 and 2*r time units spent in front of the camera.

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CHAPTER 3: SUMMARY AND CONCLUSIONS

3.1 RECAP

As extinction rates accelerate causing a rapid decline in biodiversity, there is a universal agreement from scientists that the world is facing the world's sixth mass extinction (Stork, 2010). Causes for this extinction include habitat loss, climate changes, and overexploitation. Currently, the most recent Living Planet Index (LPI) has estimated that wildlife abundance on the planet decreased by as much as 58% between 1970 and 2012 (Almond, Grooten and Petersen, 2016). For species that are unable to adapt to these changes, conservation strategies must be implemented to aid in species survival and preserving natural ecosystems. Camera traps are one method used to monitor and gather information about a population of interest. For my thesis, I (1) mathematically recreate a Random Encounter and Staying time (REST) model that derives species density from camera trap data. The REST model has been used in numerous surveys to monitor a broad range of species for conservation purposes (Warbington and Boyce, 2020; Becker *et al.*, 2021; Palencia *et al.*, 2021). For optimal conservation efforts, accurate and precise density estimates must be obtained, however this is not always easy to do (Belant *et al.*, 2019). For instance, the REST model did not give accurate and precise density estimates for domestic dogs when using Ltl-Acorn cameras (Yajima and Nakashima, 2021) due to the camera failing to meet the assumption of perfect detectability. For the second part of my thesis, I (2) used mathematics to determine how the precision and accuracy of the density results are influenced from the model parameters (animal speed, research period, detection zone area).

I found that the latest model from the camera trap literature, the REST model, will only estimate density correctly only if the model is revised using the equations I have shown about to account for the shape and size of the detection zone area. For a circular detection zone, using a correction factor of pi/8 will give unbiased density estimates. Otherwise, the density estimates will likely estimate true density to be lower than it truly is. The revised REST model shown in equation 18 will produce unbiased density estimates for true species density for circular detection zones. The REST model provides the most precise results when the research period is long, the detection zone area is large, and when it is used for fast moving animals. The accuracy of the results is true to species density regardless of camera detection zone area, animal speed, or research period. I assumed that 1) detection zone is circular and 2) animals moved ballistically, at a constant speed and same direction. All other assumptions of the REST model, outlined by Nakashima, Fukasawa, and Samejima (2018) hold true: 3) animals are not attracted nor repelled by the cameras, 4) cameras are placed randomly with respect to animal movement, 5) species density does not change within the research period, 6) inside the detection zone area there is perfect detection, 7) the distribution of staying time within the detection area represents the distribution of animal movements, 8) observations are independent events and 9) the staying time is modelled using an appropriate distribution. These assumptions could constrain the REST model's applicability if they are properly addressed, thus my work provides insight on the best practices for this model.

3.2 A HINDSIGHT REVIEW OF THE REST MODEL'S ASSUMPTIONS

The ideal-gas law is a model to determine rates of collision between gas molecules within an enclosure. Ecologists have repeatedly used the model to determine the collision rate of ecological processes such as mate finding (Crowley *et al.*, 1991), fertilization kinetics (Randerson and Hurst, 2001), and predator-prey dynamics (Vander Vennen et al. 2016). Rowcliffe *et al.* (2008) uses the ideal gas law to model animal movement patterns for the REM and similarly I use it to describe the rate that an animal will enter the camera trap detection area for the REST model. Following the gas law's formula, the REST model's expected trapping rate is a function of animal speed, camera detection zone area, research period, and species density. However, an animal's movement patterns depend on its internal state, physiological constraints and environment (Fleming *et al.*, 2014). Consequently, animals do not move ballistically as they are assumed to do in the model. Hutchinson and Waser (2007) proved analytically that even when breaking this assumption, the mean number of encounter rates remains the same as it would for ballistically moving animals, however some of those encounters will be the same individual re-entering the camera trap. The REST model gives unbiased density estimates irrespective of the number of individuals encountering the detection zone since it does not require individual identification and consequently the staying time will not be affected.

Another assumption I relied on here is that camera trap detection zones are circular. The circularity assumption was used to simplify the mathematics involved in deriving the REST model, however it is logistically unrealistic. Camera detection zones are shaped as a segment of a circle and by changing the detection zone shape, the correction factor would also change, and bias the estimates. While it is possible to map out a circular detection zone area, this would be logistically difficult. It is therefore my recommendation that future work recreate the derivations of the REST model in my thesis using a circular sector detection zone area. It is worth noting that many researchers are now shifting to placing their camera high above the ground, facing down, effectively creating a circular detection zone.

The REST model assumes that the cameras are not attracting or repelling individuals. While cameras have a longstanding history of being considered non-invasive compared to other methods, there have been numerous examples of animals detecting and investigating cameras

(Sequin *et al.*, 2003; Wegge, Pokheral and Jnawali, 2004; Schipper, 2007). Cameras can carry human scent, emit sound, and have a tangible presence within the environment (Caravaggi *et al.*, 2020) causing behavioural responses towards cameras that may affect detection probabilities (Meek *et al.*, 2014) and bias the REST model's density estimates. Almost all the density models (REST model, REM, TTE method, STE method, IS method, USCR, distance sampling using camera traps) depend on this assumption being met. One possible solution is to habituate the animals to the camera traps and truncate the data for when an animal has no behavioural responses to the camera (Caravaggi *et al.*, 2020), and to only use flash photography when necessary. If animals are reacting to cameras, it would be advisable to use a depression-angle layout for the camera traps, where cameras are situated high up (100-120 cm above the ground) so that the animals are less aware of their presence. In this way, the animal is less likely to become aware and react to the camera trap.

The study design should be carefully set up to meet assumptions 4 and 8. Cameras should be spaced far enough apart that there is independence between the cameras. Further, camera trap survey designs should not target or avoid features but be placed randomly throughout the area. Some designs that meet this criterion are the random distribution and systemic distribution. Random placement designs randomly place cameras within the survey area which do not target or avoid features. However, this survey design can potentially place cameras in inaccessible locations. Systemic survey designs, on the other hand, place cameras at evenly spaced sections. This design is not suitable for landscapes that have man-made structures built at equally spaced intervals, such as roads or logging areas. These two designs can be combined by having cameras randomly placed within a stratified grid, a design called stratified-random placement

(Nakashima, Yajima and Hongo, 2021). This would reduce the labour efforts that could potentially arise from random placement designs while still giving unbiased density estimates.

There should not be any births, deaths, immigration, or emigration occurring throughout the research period, however I have shown that having a longer research period give more precise REST density estimates. This results in a bias-precision trade-off, where each ecological system studied must balance meeting assumption 5 and optimizing the precision of the density estimates. For slow-living species, having a longer sampling period will increase the precision of the estimates without compromising bias in the estimates, however, fast-living species have high fecundity and a shorter lifespan (Dupont *et al.*, 2019). Individual traits such as an individual's sex (Clutton-Brock *et al.*, 2002), age, and behaviour influence its likelihood of immigrating, emigrating, or mortality. Closure violations have been shown to affect occupancy models (Rota *et al.*, 2009), capture-recapture models (Kendall, 1999), and in some instances spatial capture-recapture models (Dupont *et al.*, 2019). For instance, in a 3-week period, 71% of species investigated in Montana showed violation of closure (Rota *et al.*, 2009). Closure violations should be avoided, in particular for rare or declining species, where precise density estimates are essential.

Perfect detection within the detection area is a critical assumption necessary to achieve a correct staying time. Camera sensitivity is improving rapidly, with higher quality cameras having faster trigger times and greater detection zones. However, animal size (McIntyre *et al.*, 2020), movement patterns, and environmental conditions will cause detection probability to be < 1 (Yajima and Nakashima, 2021). This is an issue because most camera trap models require perfect detection for species density estimates. Without accounting for these issues, camera traps have been shown to miss animals by 3-40%, heavily biasing the density estimates (Nakashima *et al.*, 2022), and low quality Ltl-Acorn cameras missed about half the individuals (Yajima and Nakashima, 2021). Further, there is variation in detection between cameras. Researchers should note that higher placement of cameras decreases detection probability (McIntyre *et al.*, 2020), as well as cameras facing downwards (Yajima and Nakashima, 2021). To account for this, an 'independent double-observer approach' has been shown to be effective if camera traps detect animals nearly independently from one another (Nakashima *et al.*, 2022). In this method, multiple cameras each take pictures of the same area, and the detection probability is determined through the matched or mismatched observation records. This method is more costly as it requires more cameras to be installed. Another method to account for imperfect detection is to account for the effective detection distance (EDD) (Hofmeester, Rowcliffe and Jansen, 2017). The EDD is the distance at which the number of animals detected further away equals the number of animals missed nearer by, which will correct for imperfect detection within the camera trap frame of view. However, the EDD must be calculated for each camera trap and the distance between an individual and the camera must be measured using markers.

Understanding animal movement patterns is critical to meet assumption 7. Many animals regulate their activity patterns over a 24-hour sleep-wake cycle which corresponds to periods of inactivity and activity. During phases of activity, an animal will choose its movement patterns to meet its psychological needs: to mate, forage for food, or evade predators. These activity peaks occur during the day, night or in twilight hours, and are followed by phases of inactivity, when an animal is resting. Rest is a critical evolutionary behaviour to aid in energy conservation, memory retention and acquisition, and improved alertness (Roth, Rattenborg and Pravosudov, 2010). During phases of inactivity when an animal is sleeping, the probability of a camera trap detecting an animal is zero due to the animal's immobility (Nakashima, Yajima and Hongo, 2021). The REST model requires animal movements to represent the staying time of an animal's activity phases and consequently these periods of inactivity will bias the REST model's density estimates. A solution to this is to simply censor the research period to not include phases when an animal is inactive if the movement patterns of the species can be determined. Recently, Rowcliffe *et al.*, (2013) has used camera trap time-of-detection data to obtain species activity level. This model assumes that all individuals are active at the peak of the daily activity cycles which is true for only some species.

3.3 CONSIDERATIONS WHEN USING THE REST MODEL

The REST model is likely to become a popular model for field work surveys. There have been two protocols that have been created to give practical application for the REST model (Hongo, Nakashima and Yajima, 2021; Nakashima, Yajima and Hongo, 2021). Here, I outline key questions to consider when choosing the REST model for ecological research:

Is the REST model the correct model to use? There are seven additional models that do not require individual identification (N-mixture model, TTE method, STE method, IS method, USCR model, CT-DS, and REM) and one that uses individual identification (capture-recapture model). Make sure that the REST model is the best suited model for the ecological environment and study species. Low density species do not provide adequate staying times to obtain accurate REST model density estimates. Alternatively, the N-mixture model is better suited to target certain features, the STE method and IS method account for imperfect detection probability, and capture-recapture models produce better density estimates for species that have identifiable markings.

What should the design set-up be? Once you have chosen the REST model, choose one of the three design set-ups (stratified placement, random placement, and stratified-random placement) that are suitable. Cameras should be set up to optimize detection probability and be discrete in the environment. Do not use any equipment that does not match the natural environment.

How long and how many cameras? The camera model should take continuous time-lapse photographs or videos and be resilient to environmental conditions. There must be enough cameras purchased to cover the entire sampling frame and the coefficient of variation should be less than 10% (Nakashima, Yajima and Hongo, 2021). Based on simulations, between 25-100 cameras should be deployed, depending on the rarity of the species (Nakashima, Fukasawa, and Samejima 2018). Each camera's battery life should be powerful enough to allow the cameras to be left unattended for the duration of the research period to reduce labour efforts. The research period can be decided based on the desired precision of the density estimates and the life-history of the species in question. Nakashima, Yajima and Hongo (2021) recommends the Browning's camera as a camera that is both cheap and effective.

How should I analyze the data? Cameras can gather a lot of information. There have been multiple computer programs that sort out false-positive detections and organize the camera trap data (Norouzzadeh *et al.*, 2018; Willi *et al.*, 2019). The staying time of the species, the research period and the detection zone area must be calculated. Environmental covariates can be incorporated to measure species density at landscape scales (Nakashima, Hongo and Akomo-Okoue, 2020).

3.4 CONCLUSION

Camera traps are becoming more widespread as a non-invasive way to study species. The REST model is a relatively new model that uses camera trap data to estimate species density. My work adds to our collective understanding of how the REST model works, and consequently allows it to be used with confidence to estimate species density.

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APPENDIX 1: MATHEMATICAL MOMENTS

Moments

Moments is a quantitative measure of the shape of the function used to determine the mean, variance, and skewness. There are two types of moments, raw moments, and central moments. Central moments are centered around the mean whereas raw moments are centered around zero. Generally, the mean, E(x) (1st moment) is derived as a raw moment and the variance Var(x) (2nd moment) is derived as a central moment.

Raw moments

The nth raw moment $E[X^n]$, where X is the parameter in question and f(x) and p(x) are the probability functions for continuous and discrete random variables (see appendix 2), respectively, is

$$\mu'[X^n] = E[X^n] = \begin{cases} \int_{-\infty}^{+\infty} x^n f(x)dx & for\ continuous\ random\ variables \\ \sum_i x_i{}^n \cdot p(x_i) & for\ discrete\ random\ variables \end{cases}$$

n=1 gives the mean or average of the function.

Central moments

The nth central moment $\mu[X^n]$, where μ denotes the mean, is

$$\mu[X^n] = E[(X-\mu)^n] = \begin{cases} \int_{-\infty}^{+\infty} (x-\mu)^n f(x)dx & for\ continuous\ random\ variables \\ \sum_i (x_i-\mu)^n \cdot p(x_i) & for\ discrete\ random\ variables \end{cases}$$

When n=2 it gives the variance of the function. Alternatively, the central variance is equal to $Var(X) = E[X^2] - (E[X])^2$, based on Pascal's triangle rules.

Joint moments

Two independent random variables can be combined to give multivariant moments. Given random parameters X and Y, the joint mean is given as

$$E(XY) = E(X) \cdot E(Y)$$

and the variance is given as

$$Var(XY) = [E(X)]^2 \cdot Var(Y) + [E(Y)]^2 \cdot Var(X) + Var(X) \cdot Var(Y)$$

APPENDIX 2: PROBABILITY DISTRIBUTIONS

Probability distributions

Probability distributions are used to determine the probability that a random event occurs x times. There are two types of distributions, probability density functions and probability mass functions. Probability density functions are used for continuous variables and probability mass functions are used for discrete variables.

Poisson distribution

The Poisson distribution is a specific probability mass density describing the probability of the rate of occurrence of an event in each time frame, where λ is the average rate E(x) and k is the number of events within the interval. The variance of the Poisson distribution is the same as the average, set equal to λ. $E(x) = Var(x) = \lambda$. Poisson distributions are appropriate to use when the event occurrence rate is discrete, random, and constant.

$$PMF_{Pois} = P(X = k) = \frac{\lambda^k \cdot e^{-\lambda}}{k!}$$

APPENDIX 3: METHOD OF MOMENTS

Gamma distribution

Based on method of moments, it can be shown that in terms of $E[X]$ and $Var[X]$

$$E[X] = \frac{\alpha}{\beta}$$

$$Var[X] = \frac{\alpha}{\beta^2}$$

If the mean $E[X]$ and variance $Var[X]$ for the gamma distributions are given, then the corresponding α and β for the gamma distribution are given by

$$\alpha = \frac{E[X]^2}{Var[X]}$$

$$\beta = \frac{E[X]}{Var[X]}$$

We use these parameters for determining the 95% quantile (also known as the inverse cumulative distribution function) of the distribution. Quantiles specify the value of the random variable such that the probability of the variable being less than or equal to the value equals the given probability.

Weibull distribution

Based on method of moments, it can be shown that in terms of E[X] and $Var[X]$

$$E[X] = \alpha\Gamma\left(1 + \frac{1}{\beta}\right)$$

$$Var[X] = \lambda^2 \left[\Gamma\left(1+\frac{2}{\beta}\right) - \left(\Gamma\left(1+\frac{1}{\beta}\right)\right)\right]^2$$

β can be determined using computational functions to determine the optimal β that will complete the equation

$$ln\Gamma\left(1+\frac{2}{\beta}\right) - 2ln\Gamma\left(1+\frac{1}{\beta}\right) - \ln(Var[X] + E[X]^2) + 2\ln\big(E(X)\big) = 0$$

And the corresponding α is given by given by

$$\alpha = \frac{E[X]}{\Gamma\left(1+\frac{1}{\beta}\right)}$$

We use these parameters for determining the 95% quantile (also known as the inverse cumulative distribution function) of the distribution. Quantiles specify the value of the random variable such that the probability of the variable being less than or equal to the value equals the given probability.

Log-normal distribution

It can be shown that in terms of $E[X]$ and $Var[X]$

$$E[X] = e^{\mu+\frac{\sigma^2}{2}}$$

$$Var[X] = e^{2\cdot\mu+\sigma^2} \cdot \left(e^{\sigma^2} - 1\right)$$

If the mean $E[X]$ and variance Var[X] for the lognormal distributions are given, then the corresponding μ and σ^2 for the log-normal distribution are given by

$$\mu = \log\left(\frac{E[X]^2}{\sqrt{Var[X] + E[X]^2}}\right)$$

$$\sigma^2 = \log\left(\frac{Var[X]}{E[X]^2} + 1\right)$$

We use these parameters for determining the 95% quantile (also known as the inverse cumulative distribution function) of the distribution. Quantiles specify the value of the random variable such that the probability of the variable being less than or equal to the value equals the given probability.

APPENDIX 4: WEIBULL AND GAMMA CONFIDENCE INTERVALS

Gamma Distribution

Table – 95% confidence intervals using the gamma distribution of the expected range for the density estimates to fall, with the middle line being the mean estimate of density (which is the same as true density). These estimates were derived for one month, three months, and one year at three different radius sizes at the speed of 0.1 m/s.

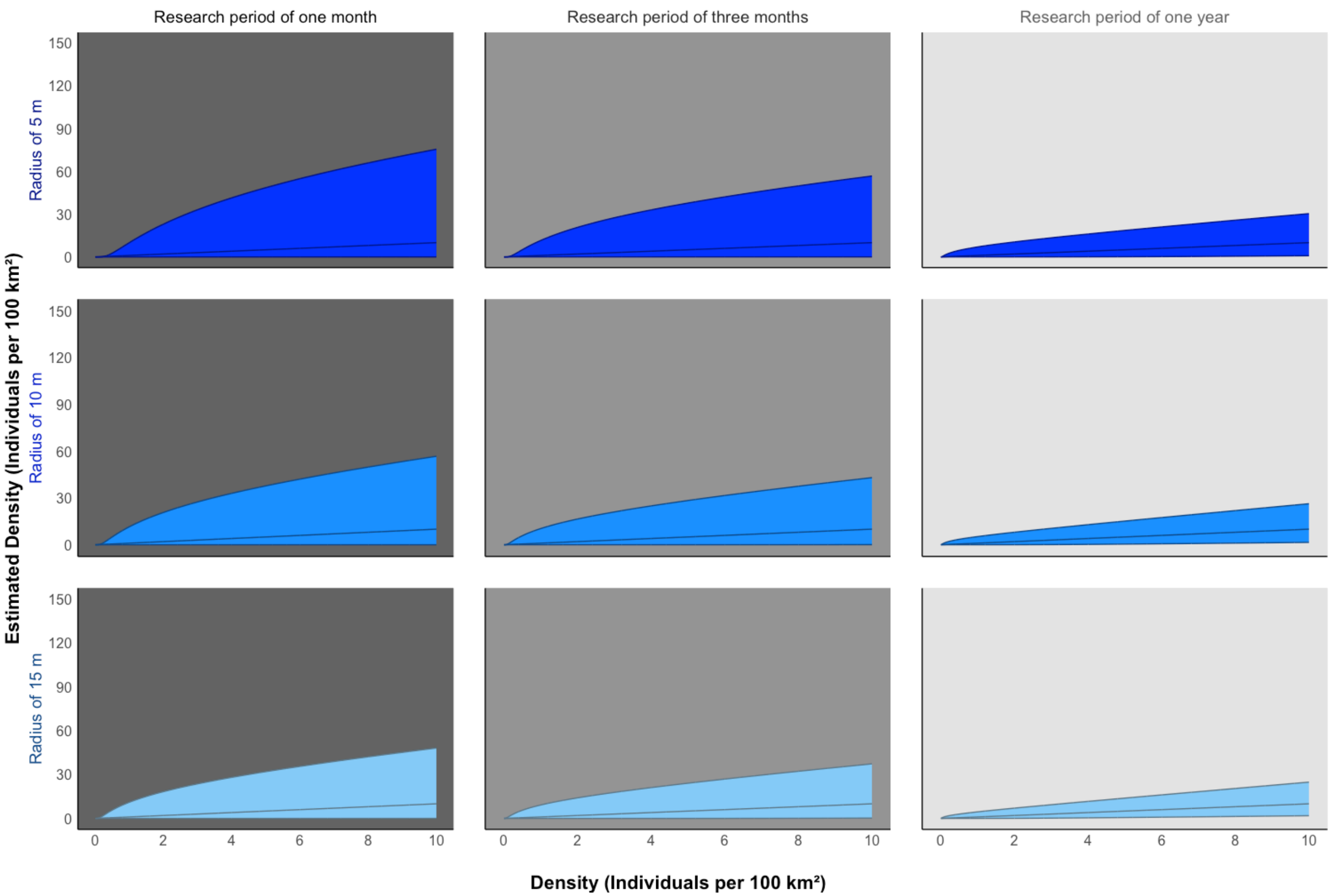


Table – 95% confidence intervals using the gamma distribution of the expected range for the density estimates to fall, with the middle line being the mean estimate of density (which is the same as true density). These estimates were derived for one month, three months, and one year at three different radius sizes at the speed of 1 m/s.

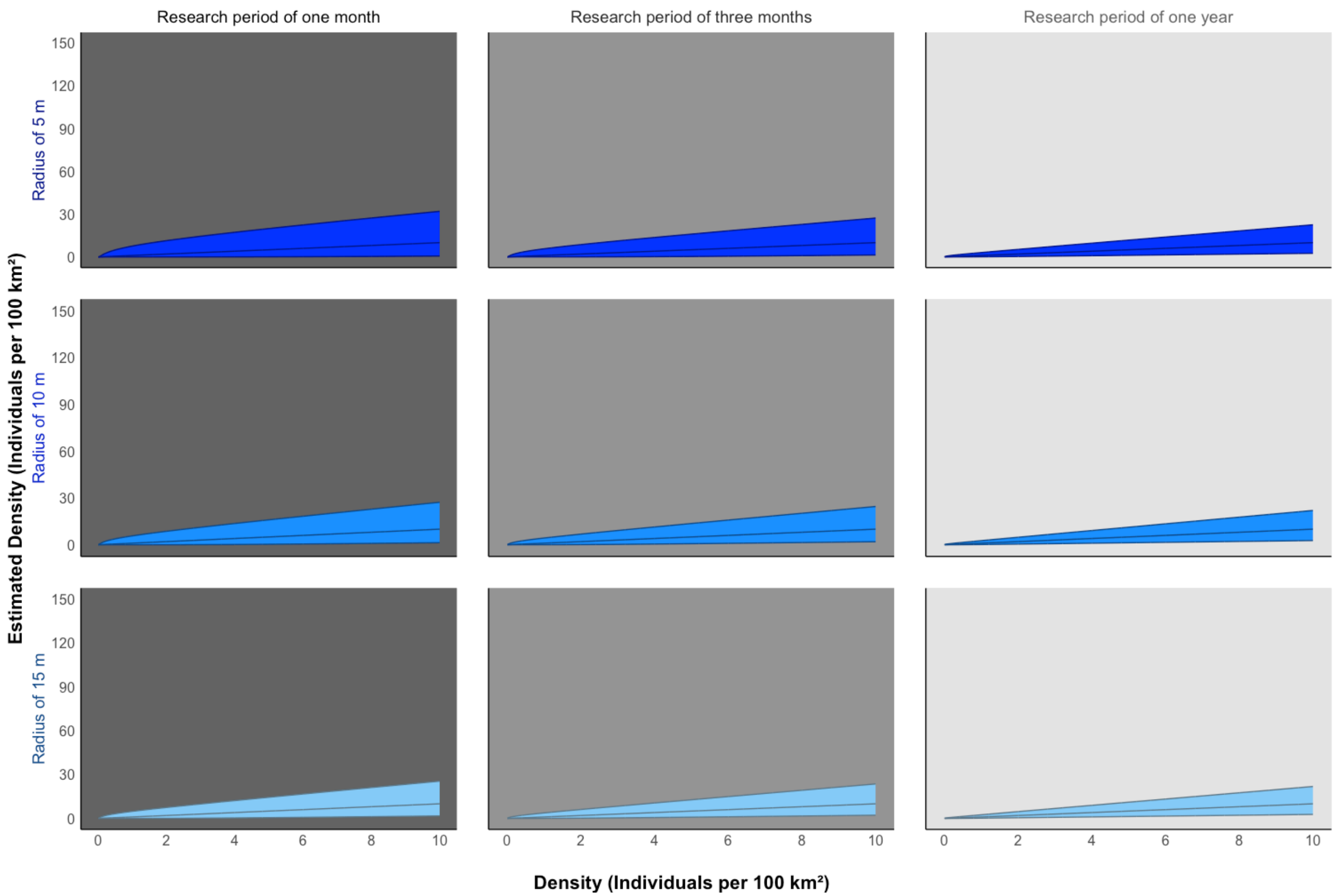
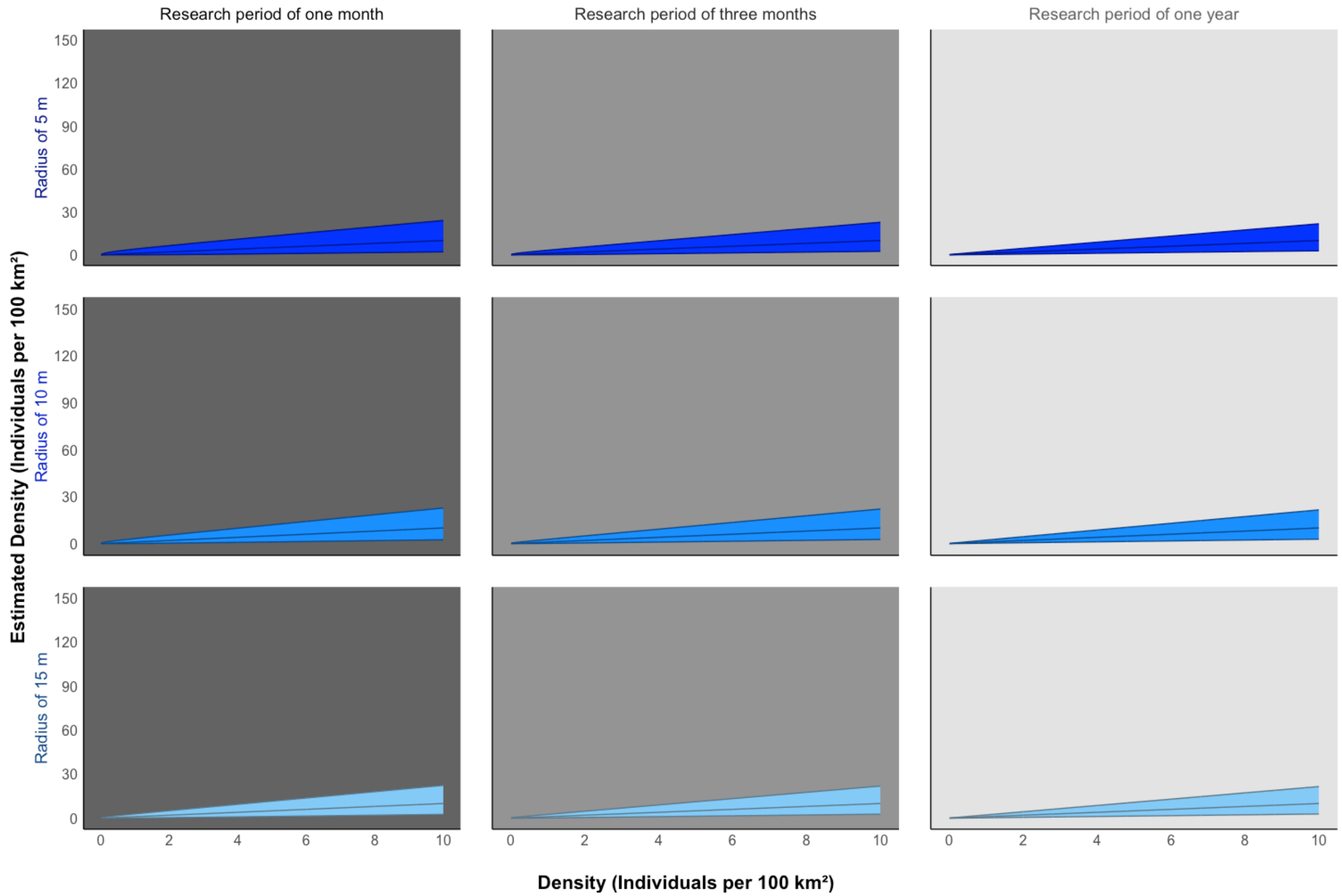


Table – 95% confidence intervals using the gamma distribution of the expected range for the density estimates to fall, with the middle line being the mean estimate of density (which is the same as true density). These estimates were derived for one month, three months, and one year at three different radius sizes at the speed of 5 m/s.



Weibull Distribution

Table – 95% confidence intervals using the Weibull distribution of the expected range for the density estimates to fall, with the middle line being the mean estimate of density (which is the same as true density). These estimates were derived for one month, three months, and one year at three different radius sizes at the speed of 0.1 m/s.

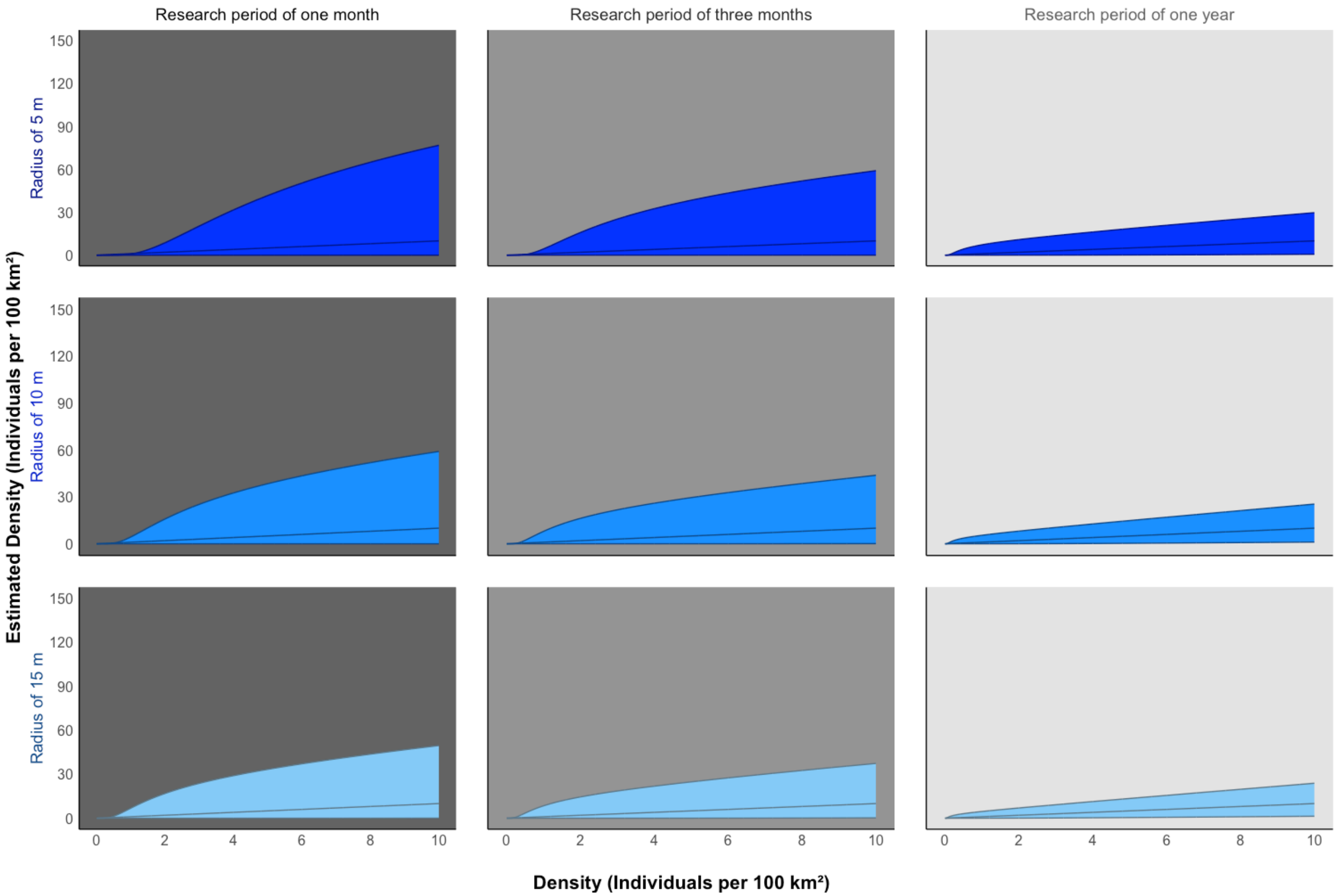


Table – 95% confidence intervals using the Weibull distribution of the expected range for the density estimates to fall, with the middle line being the mean estimate of density (which is the same as true density). These estimates were derived for one month, three months, and one year at three different radius sizes at the speed of 1 m/s.

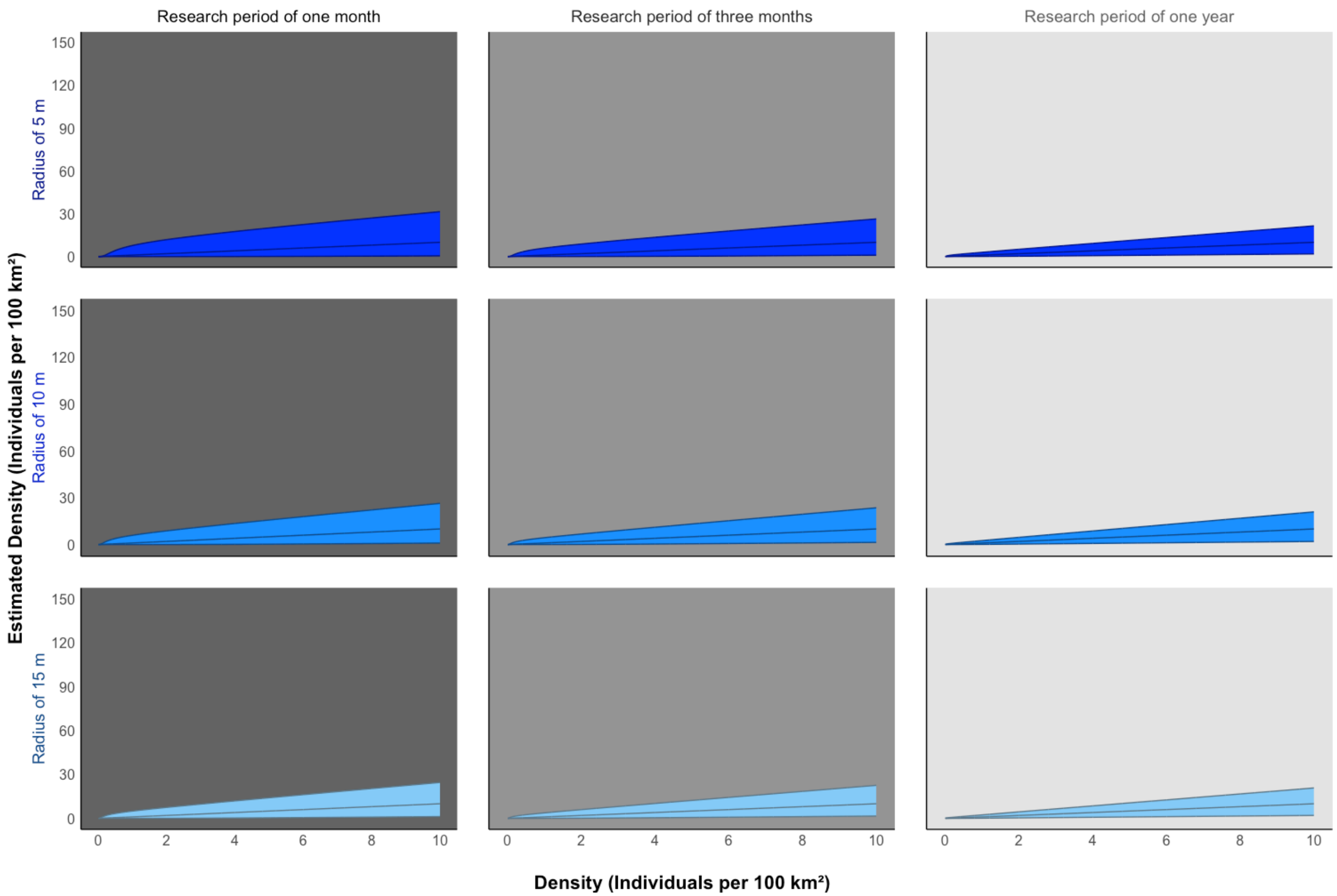


Table – 95% confidence intervals using the Weibull distribution of the expected range for the density estimates to fall, with the middle line being the mean estimate of density (which is the same as true density). These estimates were derived for one month, three months, and one year at three different radius sizes at the speed of 5 m/s.