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Best practices to account for capture probability and viewable area *in camera*-based abundance estimation

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Abstract

A suite of recently developed statistical methods to estimate the abundance and density of unmarked animals from camera traps require accurate estimates of the area sampled by each camera. Although viewshed area is fundamental to achieving accurate abundance estimates, there are no established guidelines for collecting this information in the field. Furthermore, while the complexities of the detection process from motion sensor photography are generally acknowledged, viewable area (the common factor between motion sensor and time lapse photography) on its own has been underemphasized. We establish a common set of terminology to identify the component parts of viewshed area, contrast the photographic capture process and area measurements for time lapse and motion sensor photography, and review methods for estimating viewable area in the field. We use a case study to demonstrate the importance of accurate estimates of viewable area on abundance estimates. Time lapse photography combined with accurate measurements of viewable area allow researchers to assume that capture probability equals 1. Motion sensor photography requires measuring distances to each animal and fitting a distance sampling curve to account for capture probability of <1.

Introduction

Monitoring the abundance of wildlife populations is central to the conservation and management of many species (Nichols & Williams, 2006). Advancements in remote camera technology and associated statistical methodologies in recent decades have triggered widespread application of cameras for population abundance monitoring (Burton et al., 2015; O'Connell et al., 2011). Camera traps (also referred to as remote cameras, game cameras, or trail cameras) provide many benefits to wildlife monitoring, especially when used in applications where traditional population survey techniques would be insufficient or impossible (e.g., with rare species, in remote study areas, or in dense vegetation; Karanth, 1995; Silver et al., 2004; Steenweg et al., 2017; Suwanrat et al., 2015). Early examples of estimating abundance from camera data required marked, or individually recognizable, animals and capture-recapture statistical approaches (e.g., Karanth & Nichols, 1998). However, the use of cameras for monitoring abundance became more widely feasible with subsequent development of sampling and statistical approaches to monitor abundance of unmarked wildlife populations (Gilbert et al., 2021).

Today, estimating abundance of unmarked populations remains a major focus in camera trap research, and several methods have emerged for translating observations of animals from cameras into estimates of abundance (reviewed by Gilbert et al., 2020). A subset of these methods relate animal observations to the space directly sampled by each camera's viewshed, and they result in viewshed density estimates that can be extrapolated to abundance within broader sampling frames (Gilbert et al., 2020). We refer to these here as "viewshed density estimators," and they include the random encounter model (REM; Rowcliffe et al., 2008), the random encounter and staying time model (REST; Nakashima et al., 2018), camera trap distance sampling (CTDS; Howe et al., 2017), and time to event and space to event (TTE and STE; Moeller et al., 2018).

The viewshed density estimators are all sensitive to measurements of the sampled area in front of cameras (e.g., Santini et al., 2022). Even when cameras are carefully placed to representatively sample a region of interest, these cameras sample only a tiny fraction of the total study area. As an example, consider 100 cameras placed in a 500 km^2 study area. If each camera viewshed measured 157 m^2 (45°, 20 m radius), then the collective area sampled by the cameras would be 15 700 m^2, or 0.0157 km^2, which is only 0.0031% or 1/31 847 of the total study area. Thus, small changes in camera viewshed area will have large consequences for density estimates that are extrapolated across a study region that is much larger than the collective viewshed areas. Specifically, for a given dataset, a proportional increase in measurement of a camera's sampled area will result in a corresponding proportional decrease in the density estimate (Cusack et al., 2015). Proportionally, viewshed density estimators are no more sensitive to mismeasurement than any other area-based samplers (e.g., point counts, strip transects, etc.), but small areas provide less leeway for error. For example, a 10% mismeasurement of sampled area will result in a 10% bias of the extrapolated estimate for all methods, but the same absolute amount of mismeasurement (e.g., 10 m^2) makes up a larger percentage of error for small areas than for large areas.

Although all viewshed density estimators share a fundamental component – the area sampled by cameras – explicit definition of this viewshed area, how it varies across methodologies, and how to measure it in each case remain intractable and variable across the literature. Here, we define the relevant area for viewshed density estimators, review methodologies for measuring viewshed area, and provide recommendations for future application of viewshed density estimators.

Definitions

We begin by establishing a consistent set of terms, defining how they apply to different types of photography and density estimators, and breaking apart the component parts that can change across time and space (Table 1). We use the term *viewshed* most broadly to refer to the various delineations of the area in front of a camera trap, with different specific definitions for different types of photography (time lapse and motion sensor). *Time lapse photography* occurs when camera traps are programmed to take photos at regular, predefined time intervals (e.g., every 10 min), whereas *motion sensor photography* occurs when a passive infrared (PIR) sensor triggers the camera trap to take a picture.

For time lapse photography, the viewshed is equivalent to *viewable area*. When a picture is taken, viewable area is the amount of landscape that can be seen by an observer of the photo at a resolution sufficient to identify the target species. Viewable area is affected by *viewable angle* (the horizontal angle or field of view captured by the camera lens) and *viewable distance* (how far an observer can reliably see and identify species) (Fig. 1A). Viewable angle and distance for a given camera trap can vary with camera make and model, terrain and vegetation obstructions, daylight versus nighttime flash lighting considerations, and other field conditions (Moll et al., 2020). It is important to note that viewable area is not only defined by camera and landscape characteristics, but also by characteristics of the observer, such as the individual's level of experience or attention to detail. The details of animals in photographs are harder to see the farther they are from the camera, so observers will vary in their ability to pick up those details. This means that the observer – whether human or artificial intelligence – is an integral part of the definition of viewable area. Finally, the size and characteristics of the animal itself can contribute to viewable area; larger animals and those that are easiest to identify can be recorded at farther distances than small animals that could be confused with other species.

For motion sensor photography, the viewshed is defined by the intersection of viewable area with *trigger area*. Trigger area is the area defined by the *trigger angle* and *trigger distance* within which PIR sensors can detect infrared radiation and trigger the camera to take a picture (Fig. 1B). Motion sensor photography occurs when a PIR sensor detects sufficient changes in infrared radiation (due to motion of an object) within the trigger area and triggers the camera shutter (Welbourne et al., 2016). To take a photo of an animal by motion sensor photography, the PIR sensor must detect motion in the trigger area and the animal must be within the camera's viewable area. As described by Findlay et al. (2020), each of these steps comes with some level of probabilistic uncertainty regarding whether motion will lead to a trigger and whether that trigger will lead to an animal registering within the photo. Following Findlay et al. (2020) we dub the area where the viewable area and trigger area intersect (i.e., where an animal will both trigger the sensor and register within the viewable area of the photo) to be the *registration area*, which can be defined by a *registration angle* and *registration*

Table 1. Definitions of common terms.

Term	Definition
Capture probability	The probability that an animal is captured in a photo given it is present in the camera's viewshed. For motion sensor photography, capture probability is the joint probability that the motion sensor triggers the camera shutter and the animal registers within the photo and an observer correctly identifies the species, given something passes through the trigger area. For time lapse photography, capture probability is the probability that an observer correctly identifies an animal given it is in the viewable area.
Detection probability	The probability that an animal in the broader study area encounters a camera and is captured in a photograph. Detection probability is the product of encounter probability and capture probability.
Encounter probability	The probability that an animal will pass through the viewshed of a camera given the animal is present in the study area.
Motion sensor photography	A camera function that takes photos when motion is detected in the trigger area. Infrared radiation differences between the animal and its surface environment trigger the camera to take a photograph. This is the most common means by which animal observations are gathered from camera traps in wildlife research.
Passive infrared (PIR) sensor	A sensor on camera traps that detects differences between infrared radiation of the animal in the trigger area and the infrared radiation of the surface of the environment. This sensor is sometimes called a "motion sensor" since an animal that moves into a camera's trigger area causes a difference in radiation amounts emitted to the sensor, thus triggering the camera.
Registration angle	The smaller of the viewable angle or the trigger angle, which is the angle of the area in which trigger area and viewable area overlap.
Registration area	The intersection of the trigger area and viewable area. Registration area is only applicable to motion sensor photography.
Registration distance	The smaller of the viewable distance or the trigger distance, which is the distance of the area in which trigger area and viewable area overlap.
Time lapse photography	A setting on some camera traps that sets a schedule for photos to be taken of the camera's viewshed at regular time intervals. Currently, this function is only available on certain models of camera traps.
Trigger angle	The horizontal angle of the camera trap's PIR sensor. This is often wider than the lens angle to account for any delays between activation of the PIR sensor and the camera taking a photograph while an animal continues moving.
Trigger area	The area in which PIR sensors can detect infrared radiation and trigger a motion sensor camera to take a picture.
Trigger distance	The maximum distance at which a difference in infrared radiation between an animal and its surface environment can be sensed by a camera's PIR sensor. This can be variable, depending on factors such as environmental heterogeneity, animal speed, and the configuration of the PIR sensor. Trigger distance also decays with distance from the camera's sensor.
Viewable angle	The horizontal angle of the camera trap's lens, which determines how wide of an image the camera takes.
Viewable area	The portion of the ground defined by the viewable distance and viewable angle in which animals can be reliably identified by an observer.
Viewable distance	The maximum distance in front of the camera at which animals can be reliably identified in photographs.
Viewshed	A nonspecific term referring to the sampled area in front of a camera. We use this term to refer to both registration area (for motion sensor photography) and viewable area (for time lapse photography).

distance. While the intersection of trigger and viewable areas may represent the maximum possible registration area, relative variation in the species' characteristics such as movement speed and body size as well as the speed of camera triggers may cause further reduction or heterogeneity in the functional registration area realized for a given study (Hofmeester et al., 2019; McIntyre et al., 2020).

Viewshed Area and Capture Probability

All viewshed density estimators require accurate measurement of the viewshed area to yield accurate density estimates and reliable extrapolation of density to abundance; thus, the concept of capture probability is a critical initial consideration. The terms capture probability and detection probability have often been used interchangeably with cameras because camera data are used for many different analyses whose original terms may diverge (e.g., capture-recapture and occupancy). Following the definitions proposed by Findlay et al. (2020), we distinguish capture probability and detection probability. *Capture probability* is the probability that an animal in front of a camera is captured (i.e., an identifiable photo of the animal is taken, given the animal is in front of the camera). *Detection probability* is the probability that an animal in the broader study area encounters a camera and is captured. Detection probability is the product of capture probability and encounter probability and therefore incorporates animal movement within the broader study area to the microsite of the camera. Unlike occupancy or capture-recapture, which assume that cameras sample grid cells or animal

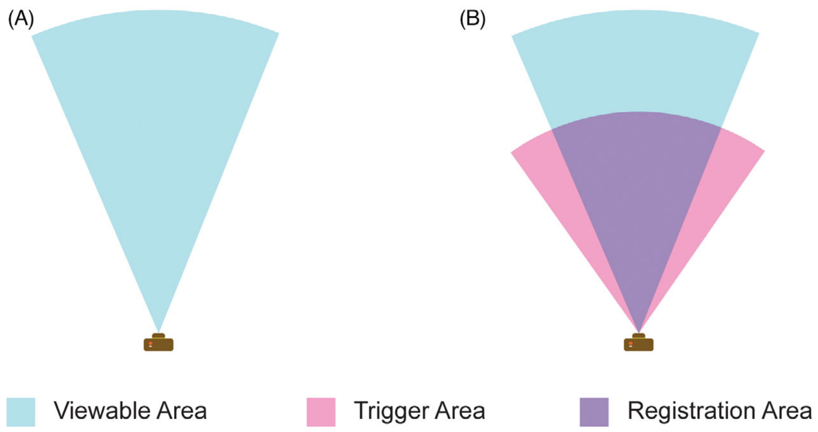

Figure 1. Visualization of viewable area (blue), trigger area (pink), and registration area for motion sensor photography (purple). (A) The viewshed area for time lapse photography is equivalent to the viewable area; (B) the viewshed area for motion sensor photography is the intersection of viewable and trigger areas, known as the registration area.

populations and therefore must account for animals that do not reach the camera, viewshed density estimators essentially work by averaging independent density estimates at different camera viewsheds. Therefore, the sampling unit is the camera's viewshed, not individual animals, and only capture probability – not encounter probability or detection probability – is relevant as defined. Viewshed density estimators assume that cameras are representative of the study area (following sampling theory principles) and cause no behavioral response (i.e., trap attraction or avoidance). Violations of these assumptions would bias density estimates. For the purposes of this paper, we will assume that these model assumptions are met, although we revisit these assumptions in the discussion.

Capture probability can take multiple forms depending on the sampling design (Findlay et al., 2020). For motion sensor photography, capture probability is the joint probability that the motion sensor triggers the camera shutter *and* the animal registers within the photo (i.e., is present in the viewable area) *and* an observer correctly identifies the species, *given* an animal or some other object (such as vegetation) passes through the trigger area (Findlay et al., 2020; Moeller & Lukacs, 2021). For time lapse photography, capture probability reduces to only one of these three components; it is the probability that a species is correctly identified by an observer, given that it is in the viewable area (Moeller & Lukacs, 2021).

Error in any of the components of capture probability would result in a capture probability of <1. A capture probability <1 would inherently bias viewshed density estimators low if naïve analyses were conducted without correction. Fortunately, practitioners of camera trap studies founded on viewshed density have developed four approaches for addressing this potential source of bias. Interestingly, capture probability and viewshed area are fully enmeshed; the methods that correct for capture probability <1 also define viewshed area.

First, camera trap distance sampling incorporates a decay function that parameterizes the reduction in capture probability with increased distance between the animal and the camera and corrects the density estimator accordingly (Cappelle et al., 2021; Howe et al., 2017). The decay function is empirically estimated for a given study using the distribution of distances associated with each photographic capture of a species during the study period (e.g., Harris et al., 2020). Designed for motion sensor photography, camera trap distance sampling inherently includes the integrated effects of viewable area, trigger area, and species-specific traits such as speed or body size. Based on the fitted decay curve, the user will choose a truncation distance beyond which any observations of animals are right truncated, and this serves as the registration distance (Howe et al., 2017). While the decay in capture probability with registration *distance* is modeled, similar decays with registration *angle* have been shown in other studies but are not parameterized with camera trap distance sampling (Rowcliffe et al., 2011). Instead, manufacturer specifications for registration angle (i.e., the smaller of the trigger angle and viewable angle) are typically used as inputs for registration angle (Howe et al., 2017), and variation in capture probability across angles is averaged together and attributed to distance alone. In cases where capture probability is functionally 0 at the outermost portions of the registration angle prescribed by manufacturer specifications (e.g., the smallest species studied by Rowcliffe et al., 2011), a slight negative bias in density estimates may be expected when using manufacturer specifications, though this has not been demonstrated to date.

A second approach to addressing imperfect capture probabilities from motion sensor data is to estimate "effective" capture distance (also called effective detection distance or EDD) and effective capture angle for input into viewshed density estimators such as the random encounter or time-to-event models (Hofmeester et al., 2017; Rowcliffe et al., 2011). Built upon the ideas of distance sampling, the effective capture distance and angle are the single thresholds in distance and angle where the number of captures missed at closer distances or narrower angles is equal to the number of captures recorded at farther distances or wider angles. Like the distance sampling approach, this approach builds probability functions based on distances and angles of animal captures to quantify the rate of decrease in captures with increasing distance and angle from the centerline of the viewshed. In contrast to distance sampling, the fitted functions are then used to estimate the single value of effective distance or effective angle using techniques akin to measuring effective strip width in standard distance sampling (Buckland et al., 2001; Hofmeester et al., 2017). When effective distances and angles are entered into density viewshed estimators, the estimates should be unbiased as if capture probability were equal to 1.

A third approach to accounting for imperfect capture probability from motion sensor photography is to use field tests or other means to estimate maximum distances and angles within which capture probability can be assumed to be 1. In some examples, trials were conducted wherein a human or domestic animal similar in size to the target wildlife species approached the camera from various angles and distances and the distance and angle of first capture were recorded (Cusack et al., 2015; Manzo et al., 2012). In these examples, the authors calculated the mean distance or angle of first capture from 10 or more trials and used these values to define registration area. However, using a value of central tendency such as the mean distance of first capture suggests that in roughly half the trials the animal was not yet captured by the time it reached the mean distance, so capture probability would still be <1. Instead, while applying the REST model to estimate viewshed density, Nakashima et al. (2018) used field trials to identify the central portion within the registration area within which capture probability was 1, and they truncated their data to retain only captures made in that area. While restricting data collection to a smaller subset of the registration area necessitates the loss of data collected outside of this viewshed definition, it facilitates much better adherence to the assumption of perfect capture probability. However, due to the uncertainties inherent in motion sensor data, it may never be possible to define an area where capture probability equals 1.

A fourth approach is to eliminate uncertainty due to motion sensors altogether by using time lapse photography to collect systematically scheduled images. In this form of sampling, capture probability is the probability that an observer can identify an individual given it is within the viewshed at the time a photograph is taken. Thus, viewshed area under time lapse photography is equivalent to the viewable area of the camera lens. Time lapse photography removes many of the factors affecting capture probability that need to be accounted for with motion sensor photography, such as animal approach angle and speed (Hofmeester et al., 2019). Each factor that affects capture probability in time lapse photography affects the viewable area alone, so there are two ways to effectively ensure that capture probability is 1. First, the observer can establish a maximum viewable distance and angle common to all photos at a camera and then truncate observations of animals outside that zone. Unlike with motion sensor photography, this method can reliably produce a capture probability equal to 1 because there is no additional uncertainty created by motion sensors. Second, the observer can measure viewable distance across time by using either landmarks at known distances (e.g., Hofmeester et al., 2017) or artificial intelligence (Haucke et al., 2022). Multiple factors affect viewable area, such as physical obstructions, weather, and time of day, and their effects on density estimation have not been quantified in the context of time lapse photography.

Motion sensor capture probability has been explored in a variety of ways, but there are no established best practices for measuring viewable area on its own, even though it is a critical component of both motion sensor and time lapse viewshed areas. Furthermore, definitions of viewable area in the literature have typically been simplistic measurements of circular sectors (e.g., Moeller et al., 2018), and there is a need to further identify and address factors that reduce viewable area in studies applying viewshed density estimators. We review considerations and methods for estimating viewable area and recommend best practices for considering it in viewshed density estimators.

Measuring Viewable Area

Calculating viewable area is a problem of geometry that can be broken down into discrete steps that depend on how cameras are positioned during setup. The most common way to deploy a trail camera is parallel to the ground, with the camera's viewable area, a, described as a circular sector (Moeller et al., 2018; Rowcliffe et al., 2008):

$$a = \pi r^2 \frac{\theta}{360} \quad (1)$$

where r is the viewshed radius and θ is the viewshed angle in degrees (Fig. 2A). An alternative, less common camera setup positions the camera at a high attachment point angled toward the ground, creating a trapezoidal viewable area (Loonam et al., 2021) (Fig. 2B). This deployment approach can be used to decrease camera theft and damage (Jacobs & Ausband, 2018). For the elevated camera setup, the trapezoidal area is calculated by:

$$a = \frac{s_1 + s_2}{2} h, \quad (2)$$

where s_1 is the width of the ground viewable at the base of an image, s_2 is the width of the ground at the top of an image, and h is the perpendicular distance between the two. In contrast to the circular sector, the trapezoidal deployment strategy results in a viewable area with definitive end points and therefore is more easily defined and measured. However, this approach has rarely been applied in camera trap research, possibly because of the greater effort required to deploy elevated cameras and a perceived decrease in animal captures (Ausband et al., 2022, although see Jacobs & Ausband, 2018).

The calculation of viewable area for either camera setup requires accurate measurements of the relevant parameters in the field (i.e., s_1, s_2, and h for the elevated camera setup and θ and r for the circular sector setup). The estimation of the trapezoidal viewable area of an elevated camera is easier to calculate of the two camera setups. The researcher can measure s_1, s_2, and h by viewing photos during deployment and identifying the outermost viewable points on the ground. These points form the edges of the trapezoid which can be measured on the ground with a tape measure (Fig. 2B). Due to the logistical challenge of repeatedly climbing up to the camera, this approach is most easily implemented with two people.

When measuring the area of a circular sector, the simplest way to determine the viewable angle θ is from the manufacturer's specifications of the lens angle, which typically falls between 35° and 55°, depending on camera make and model (TrailcamPro, 2021). It is important not to confuse the viewable angle with the trigger angle, which for most modern camera models is wider than the viewable angle of the lens (TrailcamPro, 2021). If camera specifications are unavailable, θ can be calculated by triggering the camera to take a photo, identifying landmarks on the outer reaches of the photo, then measuring the angle between the landmarks on the ground with a

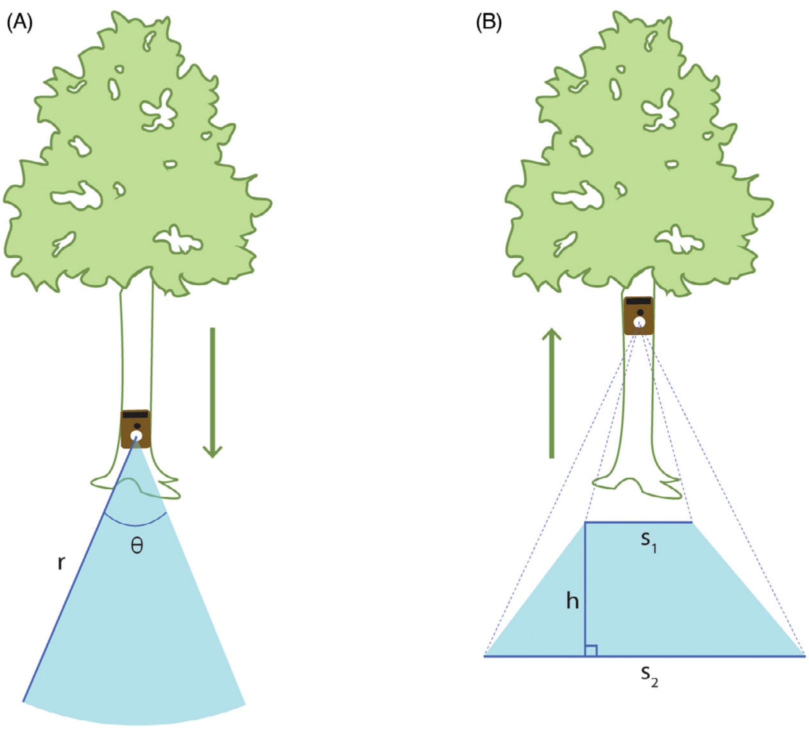

Figure 2. Viewable area geometries for two common camera setups. (A) The camera is set up parallel to the ground, typically at a lower height (indicated by down arrow), and the viewable area is a circular sector, defined by distance r and angle θ; (B) the camera is attached at an elevated position (indicated by up arrow) and pointed steeply at the ground, creating a trapezoidal viewable area defined by two parallel sides (s_1 and s_2) and the perpendicular distance between them (h).

compass. This may be time-intensive but could be accomplished prior to camera deployment if the deployed area is truly flat with an unobstructed view.

The viewable distance (r) of the circular sector is defined as the distance to which an observer can identify animals. In the simplest case of a field deployment on flat ground with an unobstructed view, the camera's viewable distance extends as far as the pixel size shows enough detail for the animal to be identified (Fig. 3A). If the camera does not capture the ground directly in front of it (due to deployment height and study species size), the viewable distance may begin a short distance away from the physical location of the camera. The observer's ability to identify animals may decay with distance, which would lead to underestimates of abundance if ignored. To account for this decay, the researcher could use some of the previously identified techniques to account for imperfect capture probability, including formulating distance sampling for time lapse photography, estimating effective capture distance, or truncating r beyond which animal observations are not recorded for analysis. In the last of these, the cutoff distance (r') is defined as the maximum distance where animals can be correctly identified in all photos, which will depend on the target species' size and identification characteristics (Fig. 3B). Once defined, the cutoff distance should be marked with flagging, posts, or other identifiable features, and animals beyond the line should be ignored during photo processing.

Equations 1 and 2 assume that cameras are deployed in flat terrain. However, this is rarely realistic, and topography creates a 3-D landscape with additional surface area. Abundance estimates are commonly extrapolated from density estimates without taking surface area into account. This is an appropriate approach so long as both camera viewable area and the study area are measured as if they were flat. This requires that distances are measured as flat-ground distances with a rangefinder or similar technique.

Vegetation, rocks, and topography can cause obstructions that restrict a camera's viewable distance. If obstructions are not factored into the calculation of viewable area, the estimated viewable area will be too large, which will lead to abundance estimates that are biased low. To account for such obstructions, one solution is to divide the circular sector into multiple, smaller sectors with smaller angles and measure the viewable distance in each sector using a rangefinder or tape measure in the field (Fig. 3C) (Idaho Department of Fish and Game, 2018). Alternatively, recent advances in artificial intelligence could be used to determine distances to objects in front of the camera. For example, Haucke et al. (2022) designed a program to measure distances to animals from a camera, which potentially could work just as well to measure distance to obstacles that dictate viewable area.

In addition to static factors like topography and obstructions, temporally variable factors have the potential to change viewable area. For instance, weather such as fog and snow may cover the camera's lens and reduce or completely restrict r and θ or s_1, s_2, and h. More consistently, viewable area likely changes with the time of day. Commonly, viewable area is reduced at night, although this may depend on the type of illumination used by the camera (e.g., white flash or infrared) and the flash strength. The viewable area can be reduced dramatically at night if reflective vegetation close to the camera renders the background completely dark. As another example, the orientation of the camera may allow the sun to shine directly into the camera early or late in the day, which reduces image quality and the distance animals can be identified in the photographs. Finally, in some systems, vegetative characteristics change with the seasons, potentially altering the viewable area over longer camera deployments that might start with leaves on but end after leaves fall. To measure viewable area that changes over time, it may be necessary to have landmarks like poles or flagging at known distances or use artificial intelligence.

Case Study

Because viewable area is reduced by obstructions, we demonstrate the practical importance of viewable area

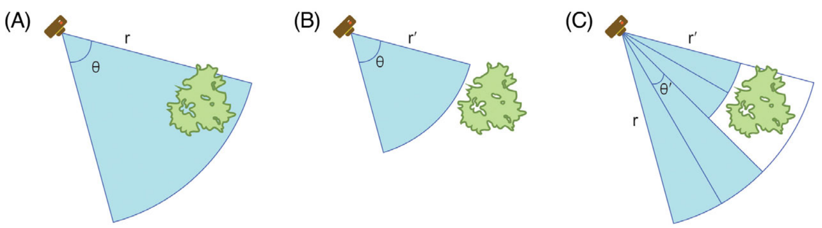

Figure 3. Alternative geometries for measuring a circular sector when viewsheds are partially blocked. (A) An example of an obstruction in the circular sector's viewable area, with nothing done to account for it. Viewable area is overestimated, which will result in abundance and density estimates biased low; (B) The cutoff distance (r') is decreased to the closest obstacle, but θ remains constant; (C) The area is divided into multiple circular sectors, each with angle θ', and the distance r or r' is measured for each.

measurements on animal density estimates using a case study from western Montana. We used time lapse photography to estimate ungulate densities during winter (21 December 2019–20 March 2020), within a 252.7 km^2 winter range study area of mixed forest and grassland. We deployed 98 cameras (models Hyperfire 2 [$n = 63$] and Hyperfire 1 [$n = 19$], Reconyx, Holmen, WI; model 119975C [$n = 16$], Bushnell, Overland Park, KS) at locations identified using generalized random tessellation stratified sampling (Fig. 4A). Cameras were programmed to take pictures every 5 or 10 min across the full study period, and motion-triggers were disabled for all cameras. Some cameras failed or were compromised prior to the completion of the study at which point data were censored from analyses. Data were aligned across cameras by subsampling to a 10-min time lapse sampling period (0:00, 0:10, 0:20, etc.) for analyses.

At each camera site, we established a maximum viewable radius of 30 m, corresponding to the nighttime flash distance of these camera models, and then divided the viewshed into 6 sectors of equal angles. Within each sector we documented all vegetation or topography features that obstructed visibility and measured their respective distances to the nearest meter. We then estimated viewshed area according to the proportion of each sector that was visible at each distance, and we treated viewshed area per site as constant over time. Visibility generally declined with increased distances from the camera as well as at the margins of the viewshed (Fig. 4B). The mean viewable area was 255 m^2, but they ranged from 74 to 328 m^2 across all cameras (Fig. 4C). Only a single site yielded the maximum viewable area of 328 m^2 without any viewshed obstructions.

We estimated density of two ungulate species, mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*), using STE analysis, following Moeller and Lukacs (2021). We applied two treatments of viewable area to our analysis: (1) we assumed capture probability was equal to 1 within the entire viewshed, out to the maximum radius of 30 m, and applied the uncorrected, maximum viewable area (328 m^2) to all camera sites, and (2) we used our field-based measurements of viewable area to correct estimates for viewshed obstructions that reduced capture probability within portions of the viewshed. We censored all observations of deer beyond the maximum radius from all analyses using field-based markers to delineate the camera viewshed boundary within pictures. The resulting data set included 893 and 651 images of white-tailed and mule deer, respectively. We estimated density and variance from the exponential likelihood (Moeller et al., 2018). We extrapolated density estimates to total abundance within the entire winter range study area according to the full area of that study area boundary.

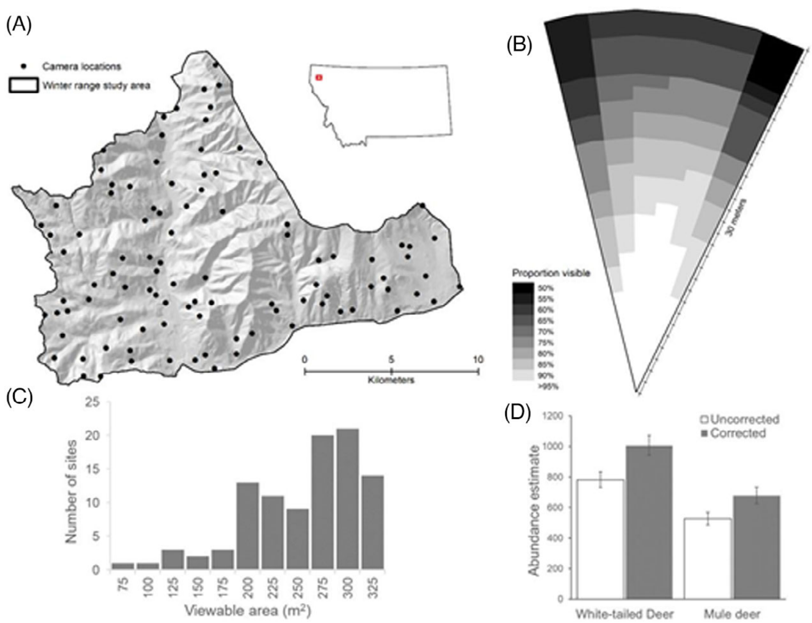

Figure 4. Methods and results of our case study in western Montana. (A) Camera locations chosen by generalized random tessellation stratified sampling. (B) The proportion of each viewshed sector visible, average across sites. (C) A histogram of the viewable area of each camera, as determined in the field. (D) Estimates and 95% confidence intervals of white-tailed deer and mule deer abundance from a space to event analysis using either the uncorrected camera area (a single, maximum viewable area applied to all cameras) or corrected camera area (measured for each camera in the field).

Uncorrected abundance estimates were 781 (95% CI 732–832) white-tailed deer and 526 (487–569) mule deer within the study area, assuming maximum viewshed area across sites. After including field-based measurements of the effects of vegetation and topography on viewshed area, corrected abundance estimates were 1006 (95% CI 944–1073) white-tailed deer and 678 (627–733) mule deer (Fig. 4D). When assuming capture probability was equal to 1, viewshed area estimates (i.e., 328 m^2) were 29% larger than the average field-measured area across sites (i.e., 255 m^2, range: 74, 328). Correspondingly, area-corrected abundance estimates were 29% higher than uncorrected estimates for both deer species. While we do not have concurrent population estimates directly aligned with this area and study period for calibration, agency biologists did observe minimum mule deer counts of 331 and 360 during two aerial surveys in April 2019 that covered a subset (63%) of this study area. Because these estimates did not correct for imperfect detection (sightability estimates averaged 57%–76% for mule deer spring surveys elsewhere in Montana; Mackie et al., 1998) and excluded deer within the remaining 37% of the study area, it suggests that true abundance of mule deer exceeds our uncorrected estimate of 526 and may be closer to our corrected estimate.

Discussion

Clear definitions of viewable area, trigger area, and registration area bring to light some practical considerations that may not be intuitive. First, because lens angle is smaller than trigger angle on many camera models and registration angle is defined as the intersection of the two, registration angle will often need to be defined by the manufacturer-specified lens angle rather than by the manufacturer-specified trigger angle or by a walk test conducted by the user. Second, measurements of trigger distance and trigger angle should never be used in calculations of viewable area, so walk tests are not an appropriate tool when the focus is on viewable area. It is important to think about viewable area and registration area as separate entities and measure the relevant components of each.

An additional example of unintuitive considerations arises when motion sensor photography is used and viewable distance is longer than trigger distance (Fig. 5). This is the case for cameras deployed parallel to the ground in open landscapes, such as food plots or grasslands. In this scenario, motion in the trigger area can produce photos of animals beyond the registration area, which must be ignored for accurate results. To demonstrate this, imagine a herd of deer present outside the registration area but inside the viewable area. Under normal circumstances, nothing triggers the camera and there is no photo record of these deer (Fig. 5B). However, motion in the trigger area (whether by another individual of the herd, an individual of a different species, or vegetation) will cause a photo to be taken and the herd suddenly becomes visible, purely by accident (Fig. 5D). If the entire herd is included in the analysis, density estimates will be biased high because animals outside the registration area were included in the data. Furthermore, because this process is inconsistent over time (animals in the viewable-only area are sometimes included and sometimes not), it has the potential to cause problems for fitting capture probability curves as needed for camera trap distance sampling and effective capture distance. This example highlights the need to exercise extreme caution when using motion sensor photography; observations outside the registration area should always be excluded.

The decision to use time lapse photography or motion sensor photography often comes down to a variety of tradeoffs (Table 2). Time lapse photography provides a perfect record of camera functionality, and given the right setup (e.g., posts or flagging to mark known distances in the photo or artificial intelligence software that can estimate distances to landmarks), viewable area can be calculated from the photos at all times. Time lapse photography results in a capture probability equal to or very near 1, but practitioners may feel concerned about its potential to produce few photos of the study species and large numbers of photos of no animals. However, the sampling unit of interest for density estimation is the viewshed area, not the animals themselves. By recording what are commonly referred to as "empty" photos, time lapse photography collects "true" zeroes, and creates a complete presence-absence dataset at a given point. Of course, for low-density species, it is possible that time lapse imagery could fail to detect the species at all, resulting in no estimate. On the other hand, when motion sensor photography is used, the same number of cameras is needed to collect a representative sample of the study area, but repeated observations of individual animals are needed to fit distance sampling curves to correct density estimates for imperfect capture probability caused by motion sensors. Therefore, motion sensor photography might produce more photos of the study species but require a hard-to-fit capture probability function to make up for complex and imperfect capture probability. Additionally, for low-density species, motion sensor photography could still fail to produce sufficient observations to fit the probability function and therefore fail to provide a robust estimate of abundance. The history of camera trap technology has led to motion sensor photography being the default choice for every type of study, including abundance and density estimation. Rather than simply choosing the default methodology, researchers should critically

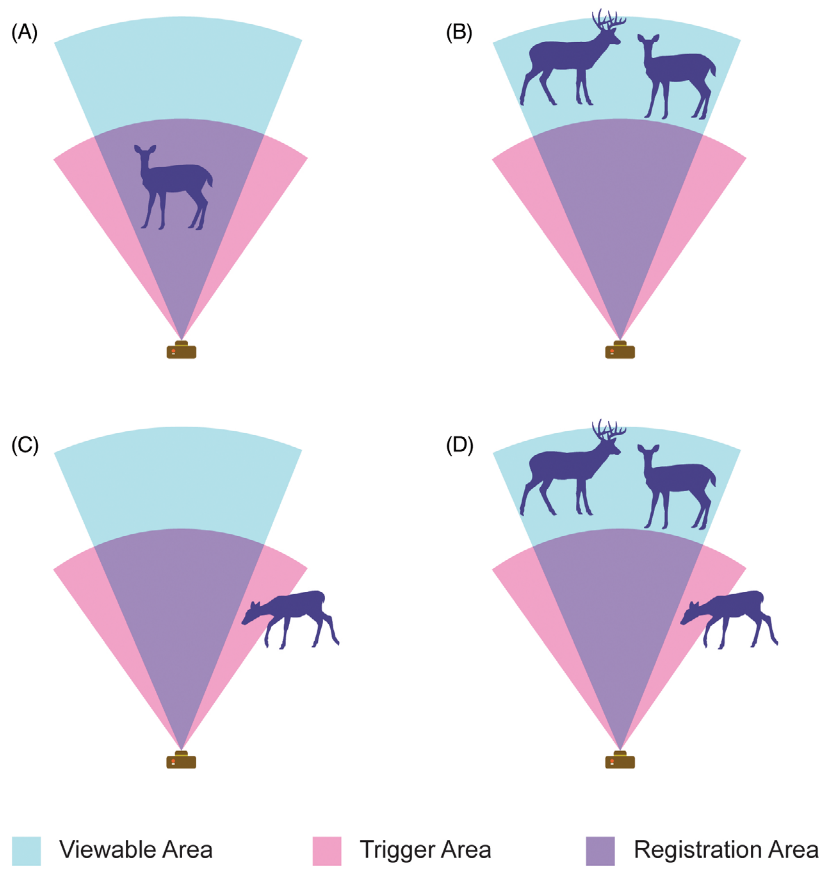

Figure 5. Patterns of photographic capture with motion sensor photography. (A) An animal enters the registration area, and a photo is taken with some probability (i.e., capture probability). This scenario is of motion sensor photography working as intended. (B) Animals are present in the viewable area only and nothing enters the trigger area, so no photo is taken. (C) An animal enters the trigger area but not the registration area, so there is some probability a photo is taken, but no animal will register in it. (D) An animal enters the trigger area, which causes a photo to be taken with some probability, and animals in the viewable-only area are captured by accident.

assess whether the information gained from a greater number of species observations is an adequate tradeoff for the information required to fit a probability function. Although motion sensor photography has deficiencies, it may be the only option in certain cases. Currently, not all camera models have the capability of taking time lapse photos, and some of the viewshed density estimators (e.g., REM and TTE) require cameras to approximate continuous sampling to meet model assumptions.

It is important to measure area for each camera separately because viewshed area can be highly variable between cameras due to location, camera model, and deployment setup (Fig. 4C). Furthermore, the assumption that photographic captures decay only with distance may not be sufficient because portions of a viewshed can be blocked by vegetation, landscape features, or topography. Some viewshed density estimators currently allow for viewsheds that change between cameras and over time (e.g., STE and TTE). Other viewshed density estimators may need to be reformulated slightly or use time-varying covariates in the fitted decay function to account for viewable area that changes over time.

As our case study illustrated, viewshed area measurements have proportional effects on animal density estimates. The assumption that the entirety of a viewshed is sampled will result in abundance estimates that are biased low in proportion with the amount of unobservable space in front of cameras, such as was observed in our estimation of deer abundance in northwest Montana. Field measurements of viewshed area can be used to correct for this bias. To obtain reliable estimates of animal density across a variety of field conditions, we recommend the same degree of care is devoted to measuring the sampled area of viewsheds that is devoted to counting the animals within them. Specifically, viewsheds should be discretely defined and measured in the field or with artificial intelligence, and photographic captures should be recorded with strict adherence to those viewshed boundaries.

Table 2. Tradeoffs for motion sensor and time lapse photography according to their relative advantages (orange) and disadvantages (red).

	Motion trigger	Time lapse
Camera model	Standard on all camera traps	Currently only available with certain models of cameras
Capture probability	Complex: PIR sensor must trigger photo + Animal captured in photo + observer must identify animal	Simple: observer must identify animal
Factors affecting capture probability	Many	Few
Certainty of absence	If no photo exists, cannot be certain if no animal entered registration area or camera malfunctioned.	Photos are always taken, so absences are certain and observers can identify times of camera malfunction
Viewshed components	Trigger area + Viewable area = Registration area	Viewable area only
Measuring viewshed area	Complex: the most accurate methods are data-intensive and time-consuming	Simple: defined by the viewable area and (most easily) a cutoff distance
Expected number of animal observations	Greatest potential for obtaining observations of study species	Observations of study species only when animals are in the viewable area at the scheduled time
Relevance of data for other research questions	Data can be used with other density estimators, as well as to investigate movement, behavior, occupancy, and competition	Has only been applied to density estimation with the STE model (but has the potential to be applied to other research questions)

Factors that affect viewshed area such as vegetation, topography, and daylight should be addressed when measuring the area sampled and identifying animal captures.

Viewshed density estimators are sensitive to mismeasurements of area (Cusack et al., 2015). Although this is proportionally no different than other area-based sampling methods, the effect may be dramatic because viewshed density estimators sample very small portions of a study area and extrapolate estimates to very large sampling frame areas. As an extension of this principle, the same magnitude of mismeasurement (e.g., undermeasuring viewshed distance by 1 m) results in proportionally more error for small camera areas than large camera areas. For example, mismeasuring a 5 m viewshed distance as 4 m underestimates area by 36%. However, mismeasuring a 10 m viewshed distance as 9 m only underestimates camera area by 19%. This means that for the same magnitude of mismeasurement, density and abundance estimates will be less biased for large viewsheds than small viewsheds. Thus, particular care should be taken to estimate the areas of small viewsheds accurately. In open landscapes, the viewable area is much larger than the registration area, so it can be advantageous to use time lapse photography and take advantage of the much larger viewshed.

When cameras are deployed representatively using the principles of sampling theory, the proportion of area sampled has no bearing on the bias or precision of the density estimate. Animals may be unevenly distributed throughout the study area (perhaps due to habitat heterogeneity), so it is important to deploy cameras using rigorous sampling design to capture a representative sample of the study area, thereby ensuring a statistically unbiased estimate. Although any one camera may have a high or low number of animal visits (i.e., differential encounter probability at different cameras due to heterogeneous animal density), the overall estimate will be unbiased if the sampling design is unbiased. Furthermore, with representative sampling, precision is derived from the number of cameras deployed and the length of time they sample, not the proportion of area covered. As heterogeneity in animal distribution increases, more cameras are necessary to achieve the same level of precision.

In addition to capture probability and viewshed area, violations of model assumptions can also influence abundance estimates. For example, behavioral avoidance or attraction to the camera (i.e., trap shyness or trap happiness) would result in biased estimates. Therefore, cameras should not be baited or deployed preferentially at high-use areas to maximize the number of photographic observations. Additionally, the methods we reviewed and described only account for animals that use two-dimensional space. They do not take into account animals that use three-dimensional space, such as climbing trees above the camera's visibility or burrowing underground below the camera's visibility. Rather than calculating density as an estimate of animals per volume (as opposed to animals per area), these animals may be considered unavailable for detection. Unavailable animals, if unaccounted for, will bias density estimates low (Amburgey et al., 2021). To address this issue, viewshed density estimators can be corrected for the amount of time that animals are available to be sampled (Howe et al., 2017).

Better estimates of density and abundance from viewshed density estimators require accurate calculations of viewable area. Viewable area is the limiting factor in the estimation of viewshed area for motion sensor photography and time lapse photography, and its importance has been underemphasized in the literature. Estimators that can use time lapse photography will benefit by using measurements of viewable area to allow capture probability to equal 1. Estimators relying on motion sensor photography should be corrected for imperfect capture probability that account for the variations in both viewable area and trigger area.

Best Practices

The factors we have considered herein enable us to provide some recommendations to researchers wanting to employ viewshed density estimators. First, research objectives and characteristics of the study population should dictate which and how many cameras are purchased. As noted previously, for low-density species, practitioners will need to maximize the number of cameras deployed, whether using time lapse or motion sensor photography. Second, tradeoffs exist between sampling with motion sensor or time lapse photography. If a distance sampling curve cannot be fit, motion sensor photography will be insufficient for density or abundance estimation; time lapse photography is the only option where capture probability is safely assumed to be 1 without additional correction. Thus, time lapse photography should be used for such applications. Motion sensor photography may be appropriate for additional study questions involving behavior, inter-species interactions, or occupancy, where issues associated with the PIR capture probability and viewshed area are not a concern. Thus, when studies can be designed for multiple purposes, including those that need motion-triggered photos, we recommend using a camera model that allows both time lapse and motion sensor triggers, although not all camera models currently allow for time lapse photography. Third, measuring viewshed area in the field or directly from photos is clearly superior to assuming that all cameras from a given manufacturer have the same viewable area once deployed in the field. This means that additional field time should be dedicated to establishing markers or reference photos at known distances during camera deployment. Finally, consideration should be given to biases caused by changing viewshed sizes during long-term deployments that could be affected by swings in weather conditions or changes in vegetative structure in front of cameras.

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