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Abundance estimation methods for unmarked animals with camera traps

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Abstract

The rapid improvement of camera traps in recent decades has revolutionized biodiversity monitoring. Despite clear applications in conservation biology, camera traps have seldom been used to model the abundance of unmarked animal populations. The goals of this review are to summarize the challenges facing abundance estimation of unmarked animals, present an overview of existing analytical frameworks, and provide guidance for practitioners seeking a suitable method. When a

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camera records multiple detections of an unmarked animal, one cannot distinguish whether the images represent multiple mobile individuals or a single individual repeatedly entering the camera viewshed. Furthermore, animal movement obfuscates any clear definition of the sampling area, and as a result, the area to which an abundance estimate corresponds. Recognizing these challenges, we identify six analytical approaches and review 927 camera trap studies published between 2014 and 2019 to assess the use and prevalence of each method. Only about 5% of the studies use any of the abundance estimation methods we identify. Of these, most studies estimate local abundance or covariate relationships rather than using models to predict abundance or density over broader areas. Next, we provide a primer on the data requirements, assumptions, advantages, and disadvantages of each analytical approach. Finally, we provide a series of considerations to help practitioners select a suitable method for their particular applications and call for a broad-scope simulation study to compare the performance of the methods under common conditions. The challenge of estimating abundance of unmarked animal populations persists despite multiple potential methodologies, as no one method appears to be the best solution for use with camera traps. As analytical frameworks continue to evolve and abundance estimation of unmarked animals becomes increasingly common, camera traps will become even more important for informing conservation decision-making.

A key frontier for camera trapping: abundance estimation of unmarked animals

Biodiversity loss is accelerating as humans exert greater pressure on natural ecosystems (Vitousek et al. 1997; Butchart et al. 2010). In response to biodiversity loss, patterns and changes in population abundance and density are critical metrics for guiding conservation decision-making (Mace et al. 2008). Traditional abundance estimation methods are challenging to implement because they usually require capturing and marking animals. In recent decades, camera traps have

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emerged as a valuable tool to monitor animal populations and represent a possible alternative to traditionally intensive methods (Fig. 1; O'Connell et al. 2011; Burton et al. 2015; Wearn & Glover-Kapfer 2019). Researchers around the world have used camera traps for diverse analytical goals, including behavior, occupancy, and species richness (Burton et al. 2015). To date, however, camera trap studies that estimate abundance focus almost exclusively on marked (individually distinguishable) animals (Fig. 1). As a result, estimating the abundance of unmarked animal populations remains a significant challenge and represents a key frontier for camera trapping.

We have three goals with this review: *1*) describe the challenges facing abundance estimation of unmarked populations; *2*) review current methods for estimating animal abundance using cameras with a focus on data requirements, assumptions, advantages, and disadvantages, and; *3*) highlight considerations for practitioners designing studies to model the abundance of unmarked animals using camera trap data.

The challenges of individual identity, animal movement, and space

Many traditional abundance estimation methods require marked individuals (Borchers et al. 2002; Williams et al. 2002). Camera trap data can be used in these frameworks in rare cases when individuals are identifiable by pelage pattern or natural marks such as scars (Karanth & Nichols 1998; Jimenez et al. 2017). However, distinguishing individuals in images or marking animals is often not feasible (but see Schneider et al. (2019) for review of emerging computer vision methods to distinguish "unmarked" individuals from images). Consequently, multiple detections of an unmarked animal at a camera could represent multiple mobile individuals or a single relatively sedentary individual. In addition, a camera will not always detect an animal that is present; therefore, an abundance estimator must *1)* disentangle the multiple-mobile versus single-sedentary problem while *2)* correcting for animals present but not detected.

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Abundance requires reference to space to be meaningful, either by reporting the area to which an abundance estimate corresponds (e.g., “we estimated an abundance of 10 squirrels in the 5 km^2 reserve”) or by estimating population density (e.g., “we estimated a density of 2 squirrels per km^2”). However, the *effective sampling area* of a camera—the area that a camera samples, given how far detected animals move—is generally unknown because animal movement information is usually not known (Fig. 2). Consequently, the *sampling frame*—the broader study area about which we wish to make inference—is generally also unknown (Fig. 2). Various methods address the challenge of space in one of three ways. First, some methods estimate abundance at camera locations without any reference to space, meaning that one must assign the estimate to an arbitrary area (Fig. 2A). Second, some methods estimate abundance within an area explicitly defined in the model by accounting for *where* and when animals are detected (Fig. 2B). Third, some methods estimate density within the collective *viewsheds* of cameras, which are assumed to be representative of the sampling frame (Fig. 2C-E). Depending on the method, the viewshed is defined as either *1)* the area within which animals can be detected by a camera’s motion sensor (*detection viewshed*) or *2)* the total area photographed by a camera (*total viewshed*).

Methods to estimate abundance or density from camera trap data

Here, we provide an overview of abundance estimation methods for unmarked animals that can be applied with camera traps. We review the data requirements, assumptions, sampling requirements, extensions, advantages, and disadvantages of the following methods: site-structured models (including *N*-mixture and Royle-Nichols models), unmarked spatial capture-recapture, the random encounter model, the time-to-event model, the space-to-event and instantaneous sampling models, and distance sampling (Table 1). We assembled this list of methods as an exhaustive list of abundance estimation methods that do not require identification of individuals.

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Relative use of methods in recent literature

We completed a literature review to assess the relative prevalence of the reviewed methods in published camera trap studies. We used Web of Science to search for papers published between 2014 and 2019 using the following search terms: (camera trap* OR remote camera*) AND (wildlife OR mammal* OR bird*) (Burton et al. 2015). We completed the search on 2 May 2019 and reviewed the returned 1,150 papers. We omitted studies that did not use camera traps, exclusively presented review, or were purely methodological (e.g. developing software). We reviewed the 927 papers that satisfied these criteria and noted *1*) whether the study used any of the methods we reviewed and *2*) whether the population studied was unmarked. For studies that used the methods we reviewed, we noted *3*) the inferential goal of the study (estimating abundance/density, quantifying covariate relationships, and/or predicting abundance/density at unsampled locations). Furthermore, we evaluated *4)* whether each study listed or evaluated model assumptions. We classified a study as having evaluated assumptions if it *a)* deployed cameras in such a way to satisfy model assumptions, *b)* modified analyses to test or account for possible assumption violation, or *c)* discussed possible assumption violation and implications for interpretation.

Only 51 studies (5.5%) used the methods that we reviewed for estimating abundance (Fig. 1). Of the 876 (94.5%) other studies, the most frequent analytical focuses were indices of relative abundance (310; 35.4%), behavior (304; 34.8%), occupancy (181; 20.7%), and species richness (178; 20.3%). Indices of relative abundance based on detection rate remain the default analytical option for many practitioners (Sollmann et al. 2013b; Burton et al. 2015). Of the 51 studies that used the methods we identified, 22 (43%) used the Royle-Nichols model, 14 (27%) used the random encounter model, 13 (25%) used *N*-mixture models, and 4 (8%) used unmarked spatial capture-recapture. The former three methods were the earliest to appear in the literature (2003, 2008, and

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2004, respectively); thus, their prevalence in our sample is unsurprising. We did not capture any studies that used distance sampling, the time-to-event model, the space-to-event model, or the instantaneous sampling model, beyond the publications that introduced these methods. The majority (39; 76%) of studies using the reviewed methods reported abundance or density; fewer studies (21; 41%) reported covariate relationships; only 3 (6%) predicted abundance over a broader area. Finally, 28 (55%) of the studies listed model assumptions, and only 23 (45%) evaluated assumption violations in some way.

An overview and description of available analytical methods

Site-structured models. Site-structured models use replicated survey periods at independent locations (termed “sites”) to jointly model ecological and observational processes (Kéry & Royle 2015). These models estimate abundance at each camera location, but because animals move beyond the detection viewshed, the effective sampling area of each camera location is some larger unknown region (Fig. 2A). Under the umbrella of site-structured models, the Royle-Nichols (RN) model (Royle & Nichols 2003) requires binary detection/nondetection data (whether or not a species is present in any photos during each replicate survey period), while *N*-mixture models (Royle 2004) require count data (the number of animals present in photos during each replicate survey period).

Both models assume population closure of the site (no individuals enter or leave the population via birth, immigration, death, or emigration), that detection probability is equal for all individuals, no false positive detections (i.e., misidentifications or double counting of individuals), and that detections of individual animals at a camera are independent (Table 1; Royle & Nichols 2003; Royle 2004). Practically speaking, the latter assumption implies that once an animal is detected by a camera, it is not any more likely to be detected during subsequent replicate survey periods. Site-structured models do not require random camera placement, meaning that cameras

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can be placed on trails or baited. However, cameras should be spaced far enough apart that individuals are not detected at multiple cameras to ensure there is no overlap in the effective sampling areas of cameras. Either method can be extended to jointly analyze data for multiple species (Yamaura et al. 2011, 2012) or open populations (Dail & Madsen 2011; Rossman et al. 2016). *N*-mixture models can be extended to accommodate correlated detections (Martin et al. 2011). The RN does not perform well for common species because the binary detection histories will be saturated with 1's and therefore contain little information; in such cases, count data used with *N*-mixture models is preferable (Kéry & Royle 2015; Dénes et al. 2015).

Site-structured models have the advantage of quantifying spatial variation in abundance as a function of covariates. However, site-structured models have the major disadvantage that the effective sampling area of cameras is unknown (Fig. 2; Kéry & Royle 2015). Consequently, predicting abundance (based on covariate patterns) across the remainder of the sampling frame or beyond is difficult and can only be done by arbitrarily defining predictive grid cell sizes (Fig. 2A). Finally, site-structured models are sensitive to assumption violations (Barker et al. 2018; Knape et al. 2018; Link et al. 2018; Duarte et al. 2018). For example, Link et al. (2018) demonstrated that minor closure violation caused biased abundance estimates that could not be detected with goodness-of-fit checks. These limitations suggest that, unless their assumptions can be verified, site-structured models should be treated as indices of relative abundance.

Unmarked Spatial Capture-Recapture (USCR). USCR is part of the spatial capture-recapture family of models, which estimate density by considering when and *where* animals are detected within an array of detectors (Fig. 2B; Royle et al. 2014). Unlike traditional forms of spatial capture-recapture that require marked animals, USCR treats the individual identities of animals as latent variables (Chandler & Royle 2013; Royle et al. 2014). USCR estimates density by modeling the number and distribution of animal activity centers as a realization of a spatial point process within

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the state space, an explicit region of inference defined within the model (Fig. 2B; Royle et al. 2014). USCR requires spatially correlated detection data—meaning that individual animals must be detected at multiple cameras—to make inference about the number and locations of the activity centers (Chandler & Royle 2013; Ramsey et al. 2015).

USCR assumes that the activity centers of individuals do not move, that the activity centers exhibit no attraction or repulsion, that animals will be detected less frequently as the distance between their activity centers and a camera increases, and that the sampling frame contains all of the activity centers of animals detected by cameras (Chandler & Royle 2013). Unlike site-structured models that require cameras to be independent, USCR requires arrays of cameras spaced such that individuals are detected at multiple cameras, though the counts at individual cameras are assumed to be independent from one sampling occasion to the next (Table 1; Fig. 2B; Chandler & Royle 2013).

USCR has the advantage of estimating abundance within a clearly defined area, thereby avoiding the unknown area problem of site-structured methods. Additionally, Evans & Rittenhouse (2018) extended USCR to incorporate spatial variation in density as a function of covariates, though further research is warranted to corroborate the robustness of such an approach. USCR has the disadvantage of being computationally expensive and restricted to Bayesian frameworks, which may be a barrier for some practitioners (Royle et al. 2014). Furthermore, USCR produces highly imprecise density estimates (Royle et al. 2014; Augustine et al. 2019) and is sensitive to choice of priors on σ, a parameter which can be interpreted as the spatial scale over which a camera detects an individual (Sun et al. 2014; Burgar et al. 2018). Finally, USCR is sensitive to assumption violations; density estimates will be biased if animal density and camera spacing relative to animal movement fall beyond a narrow range of values (Ramsey et al. 2015; Augustine et al. 2019).

Random encounter model (REM). The REM treats individual animals like ideal gas particles and estimates density within the collective detection viewsheds of a camera array (Fig. 2C). The REM

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estimates density from encounter rates (number of photographs from cameras per unit time), animal movement speed, and the camera's detection viewshed, which consists of the radius of the effective detection zone and the horizontal angle of view (Rowcliffe et al. 2008).

Importantly, the REM assumes that cameras are placed randomly relative to animal movement, meaning that cameras should be randomly deployed within habitat classes proportional to their use by animals and not target features that attract animals (e.g., trails). Additionally, the model assumes population closure of the sampling frame and that individual animals move independently of one another; for species that travel in groups, the average group size is required (Rowcliffe et al. 2008). Finally, the REM assumes that individual photos represent independent contacts between an animal and a camera (Table 1; Rowcliffe et al. 2008).

An advantage of the REM is that it estimates density for a clearly defined area—the collective viewshed of cameras. However, extrapolating to the abundance for the sampling frame is problematic because the sampling frame must be arbitrarily defined unless the study targets a region with impermeable boundaries (e.g., an island; Fig. 2C). A further disadvantage of the REM is that it requires data that are difficult to measure, specifically animal movement speed (requiring telemetry or intensive observations of behavior) and detection viewshed (requiring measurement of detection zone in the field, calibrated to species of different sizes). Another disadvantage is that the REM does not allow inference about spatial variation in density, thus inhibiting covariate-driven prediction of density beyond the sampling frame. Finally, assumption violations, particularly non-random camera placement relative to animals, leads to biased estimates. For example, Cusack et al. (2015) used the REM to estimate African lion density and found that cameras placed beneath shade trees (which attracted lions) led to biased estimates compared to a comprehensive population census. They overcame the bias by discarding daytime data and using only nighttime data when lions exhibited less attraction to trees (Cusack et al. 2015). The REM has recently been extended to the random encounter and staying time (REST) model, which does not require animal movement data—

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instead, the model relies upon staying time, which is the amount of time an animal remains within the viewshed (Nakashima et al. 2018). Staying time can be measured either from videos or consecutive photos (Nakashima et al. 2018). Additionally, the REST model can accommodate spatial variation in density as a function of environmental covariates (Nakashima et al. 2020). These advances suggest that the REST model may replace the REM in terms of feasibility and utility, though the same assumptions and sampling design considerations apply (Nakashima et al. 2018).

Time-to-event (TTE) model. Like the REM, the TTE model uses detection rate and animal movement data to estimate density within the collective detection viewshed of cameras (Table 1; Fig. 2C; Moeller et al. 2018). Specifically, the TTE model uses the time (defined as the number of sampling periods) until the first detection of an animal within a longer sampling occasion (which can start at an arbitrary moment) to estimate density (Moeller et al. 2018).

The TTE assumes population closure of the sampling frame, that camera locations are random relative to animals, and that animal detections are independent both in space (e.g., once an animal is detected at one camera, it is not any more likely to be detected by a neighboring camera) and time (e.g., an animal will not linger in front of a camera). Finally, in its current formulation, the TTE model assumes that detection is perfect.

Unlike the REM, the TTE has the advantage of accommodating spatial variation in abundance across cameras with covariates (Moeller et al. 2018), which enables predictive modeling across the remainder of the sampling frame. However, the TTE has the disadvantage of relying upon restrictive assumptions. In particular, perfect detection is rarely a valid assumption for motion-triggered cameras. The TTE also relies heavily upon the assumption that animals are distributed according to a Poisson process; any consequences of violating this fundamental assumption have yet to be demonstrated. Additionally, while the density estimate clearly corresponds to the collective viewsheds of individual cameras, inference about the sampling frame requires arbitrary definition of

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the sampling frame's area. For example, Moeller et al. (2018) defined the sampling frame of their empirical example as a 2-km buffer around GPS fixes of an elk herd. In real-world applications, practitioners seldom have GPS-marked animals to define a biologically meaningful sampling frame, and moreover, placing a buffer around GPS points can be problematic and is analogous to defining the effective sampling area of cameras with site-structured methods. Generally, the difficulty of defining a sampling frame hampers predictive modeling of density beyond the sampling frame. Finally, simulations by Moeller et al. (2018) suggested that the TTE is negatively biased, particularly for slow-moving species.

Space-to-event (STE) and instantaneous sampling (IS) models. The STE model is an extension of the TTE model but instead uses time-lapse photos; that is, cameras must be programmed to take photos at predefined times, regardless of whether an animal is present or not (Fig. 2D). The IS is a further extension of the STE that uses counts of animals in view of each time-lapse photo (Moeller et al. 2018).

Both methods share the assumptions of the TTE model; however, the assumption of perfect detection is likely more tenable with time-lapse photos. Additionally, the STE and IS rely upon the total viewshed (in a time-lapse photo, an animal may be detected beyond the distance at which it would trigger the motion sensor), meaning the viewshed must be measured based on the maximum distance at which animals can be identified, likely with the help of natural landmarks (Moeller et al. 2018). The STE estimates density from space (the number of cameras) until the first animal detection at a given moment in time (Moeller et al. 2018).

The STE and IS have the advantage of not requiring animal movement data; density estimates are independent of animal movement because each sampling occasion is a snapshot moment in time. An additional advantage is that simulations demonstrate that the STE and IS are unbiased and seem to be robust to some variation in movement rate and population density

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(Moeller et al. 2018). A major disadvantage is that time-lapse photos may make few or no detections of rare species, disqualifying STE and IS as options for such species. Additionally, neither STE or the IS model can accommodate heterogeneity in abundance across cameras. Therefore, predicting abundance (within the sampling frame and beyond) is problematic. Finally, as with the TTE model, while the density estimate clearly corresponds to the collective viewsheds of cameras, making inference about the abundance of the sampling frame relies heavily upon design considerations.

Distance sampling (DS). Distance sampling is a well-developed class of methods for estimating population density (Buckland et al. 2001). Broadly, DS involves surveying transects or points, estimating the distance to detected animals, and fitting a detection function to the estimated distances, which allows the number of undetected animals to be estimated (Buckland et al. 2001; Borchers et al. 2002). Unlike traditional DS surveys in which observers move relative to animals, camera-based DS surveys involve stationary detectors that survey moving animals (Howe et al. 2017). The Howe et al. (2017) formulation of DS requires measurement of each camera's detection viewshed, a calibrated measurement of the distance to the detected animal in each photo, and a measure of temporal sampling effort across all cameras (Fig. 2E; Hofmeester et al. 2017; Howe et al. 2017).

DS assumes are that detectors are randomly located relative to animals, animals at distance 0 are perfectly detected, that animals are detected at their initial location, that distances are measured accurately, and that detections are independent events in space and time (Table 1; Buckland et al. 2001). Camera traps must representatively sample the focal landscape and not target trails or other features that attract animals (Buckland et al. 2001; Howe et al. 2017).

Like several other methods (Fig. 2C-E), DS has the advantage of estimating density within a clearly defined area (the collective camera viewsheds), though making inference about the sampling frame requires strong assumptions about sampling design. DS has the disadvantage of requiring data

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that may be difficult to collect (viewshed, distances). Additionally, the Howe et al. (2017) formulation of DS does not permit inference about spatial variation in density, either within one camera array or across a sampling frame encompassing multiple arrays (Kéry & Royle 2015). Consequently, predictive mapping of abundance within or beyond the sampling frame based on covariate models is not possible. Hierarchical distance sampling permits modeling spatial variation in abundance as a function of covariates, but hierarchical DS has yet to be implemented with camera traps (Kéry & Royle 2015). Finally, DS is unbiased only when the study species is active and available for detection; researchers must account for the target taxon's activity pattern and censor times when animals are not active or available (Howe et al. 2017; Cappelle et al. 2019).

Practitioner considerations

Over the past 15 years, several methods have emerged to model abundance of unmarked animals from camera trap data. The intricacies of each method and the inconsistencies among them can be overwhelming for practitioners. Therefore, we provide a series of considerations that will guide practitioners to the method most appropriate for their application (Fig. 3).

What is the focal species? While camera traps offer the opportunity of broad-spectrum monitoring of multiple species simultaneously (Burgar et al. 2019; Wearn & Glover-Kapfer 2019), interspecific variation in life history traits renders multispecies abundance estimation problematic. When planning a study, researchers should select a focal species (or a group of species with similar traits) and use knowledge of its life history to inform study design. First, how much space does an individual use over the timeframe of the study? One can find home-range estimates and movement behavior in the literature for many species. Such information is helpful for defining a sampling frame or determining the proper spacing of cameras. For instance, "site-structured" models assume that camera locations are independent, meaning that individual animals should not be detected by

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multiple cameras; one could space cameras at least twice the diameter of an animal's home range apart to ensure that individuals are not detected by multiple cameras. Second, how does the species use features of the landscape? Several of the methods (Table 1, Fig. 2C-E) require that cameras be located randomly relative to animal distributions. If a species uses forest 75% of the time and prairie 25% of the time, randomly selecting camera locations without stratifying proportional to habitat use will result in nonrandom camera positions relative to animals. Third, roughly how common is the species? For a common species, methods requiring random camera placement or time-lapse photos may be appropriate, whereas a rare species may require nonrandom camera placement or bait to even be detected (Moeller et al. 2018). Finally, we note that multispecies abundance estimation requires careful study design to be well-founded. For example, Rich et al. (2019) estimated densities of seven marked species by employing a hybrid sampling design: half of the cameras were placed systematically with wide spacing (thus permitting density estimation for wide-ranging species), and the other half were placed randomly within the same area (thus falling within a range of distances of the systematic cameras, permitting density estimation for smaller-ranging species). For multiple unmarked species with different movement behavior, one could perhaps subset camera locations to account for differences among species, but the bottom line is that no single survey design is optimal for all species (Rich et al. 2019).

What is the focal area? Prior to selecting a method, practitioners should consider the size of the study area relative to animal movement. For example, if 50 cameras are available and the sampling frame is small (e.g., a 5 km^2 reserve for a medium-bodied mammal), site-structured models are not appropriate because animals will surely be detected by multiple cameras. Instead, STE or DS approaches may be better choices, or USCR if the extent of animal movement is contained by the sampling frame (Fig. 3; Table 1). However, if the sampling frame is an entire province (e.g., 5,000 km^2), a site-structured approach is an option since cameras can be placed at distances greater than the distances moved by individual animals. Additionally, practitioners should consider whether

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predicting abundance within areas not sampled by cameras should be an objective of their study. Prediction requires quantifying spatial variation in abundance as a function of covariates, which cannot be accommodated by all methods (Table 1).

Is relative abundance sufficient? Given the pitfalls of abundance estimation, researchers should evaluate their objectives to determine if an index of *relative abundance* is a viable alternative to estimating *absolute abundance* (Fig. 3; Yoccoz et al. 2001). An index of relative abundance can be any variable that strongly correlates with absolute abundance (Johnson 2008). Relative abundance can be a helpful state variable to guide management and conservation efforts, particularly when estimating species-environment relationships are the primary objective rather than estimating population size. For example, one could say, *"Relative abundance/activity of swift foxes was highest in prairies with low amounts of woody vegetation. Therefore, conservation strategies should focus on reversing shrub encroachment."* However, relative abundance should be avoided when absolute abundance is required (e.g., evaluating endangered species recovery).

In the world of camera trapping, indices of relative abundance are usually based on detection rate, e.g., the number of detection events per 100 trap days, and are widely used in the camera trap literature (Rovero & Marshall 2009; Burton et al. 2015). Indices based on detection rate should be applied and interpreted judiciously, since they confound abundance and animal movement (Broadley et al. 2019). As such, abundance indices based on detection rate make strong assumptions that movement behavior does not change over space or time (Sollmann et al. 2013b; Broadley et al. 2019). Ideally, researchers should calibrate detection rates—preferably to abundance estimates from independent methods—rather than blithely adopting them as replacements for abundance (Rovero & Marshall 2009; Sollmann et al. 2013b). Beyond detection rates, any of the methods we reviewed can be considered indices if their assumptions are violated. Even as indices, these methods provide advantages over indices based on detection rate; one can, for example, partially account for the observation process by using a model that includes detection probability

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(Sollmann et al. 2013b; Dénes et al. 2015). If one suspects that assumptions are violated, we recommend reporting the possible violations and reporting results as relative rather than absolute abundance (Fig. 3).

Can any individuals be marked? Abundance estimation methods that draw upon the identity of individuals are the gold standard. Traditional methods require that all individuals captured be identifiable to individual (Borchers et al. 2002; Royle et al. 2014), but emerging methods accommodate partially marked samples (Royle et al. 2014). This could be the case when only a few animals within a population are marked or when only a subset of individuals can be identified from natural markings in photos (Fig. 3). The most promising methods for partially marked populations are spatial mark-resight models, an extension of the unmarked spatial capture-recapture method presented above (Chandler & Royle 2013). Simulations demonstrate that increasing numbers of marked individuals increases the accuracy and precision of parameter estimates (Chandler & Royle 2013). A further extension of spatial mark-resight models accommodate partially identifiable individuals—for example, individuals that can be classified into categories such as sex or age group (Augustine et al. 2019). Such categorical marks can increase the reliability and precision of parameter estimates (Augustine et al. 2019). Finally, we note that marking animals opens the possibility to using integrated population models, which combine demographic data (e.g. telemetry or mark-recapture) with detection data in a single model (Schaub & Abadi 2011; Sollmann et al. 2013a; Zipkin & Saunders 2018).

What other ancillary data can be collected? If marking animals is not feasible, practitioners should evaluate the types of ancillary data that can be collected (Fig. 3). The three major forms of ancillary data used by the various methods are animal movement, distance to detected animal, and area of camera viewshed (Fig. 2). Animal movement is required for the random encounter model and the time-to-event model. Barring intensive behavioral observations or movement data gleaned from the literature (Rowcliffe et al. 2008), animal movement data requires placing radio or GPS tags

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on animals, tantamount to marking individuals. If animals must be marked to collect movement data, spatial mark-resight approaches are preferable to the REM and TTE model. Distance to detected animals is required for use with distance sampling; collecting this information requires either placing distance markers in the field (Hofmeester et al. 2017) or extracting distance *ex situ* from calibrated reference photos (Caravaggi et al. 2016). Finally, the area of camera viewsheds is required for several methods (Fig. 2). In practice, viewsheds are challenging to measure because a camera's effective detection distance will vary based on vegetation surrounding the camera, weather conditions, and the size of the animal triggering the sensor (Manzo et al. 2012). Finding ways to automate measurements to detected animals and the area of camera viewsheds would be a fruitful way to increase the feasibility of models requiring these ancillary data.

Moving forward: validating methods via simulations and empirical comparisons

Multiple unmarked abundance estimation methods exist and many more will surely emerge. Therefore, a crucial question for practitioners is, *which method can we trust to provide accurate abundance estimates, and under what conditions?* We therefore suggest *1)* a set of simulation studies to evaluate the performance methods under common conditions and *2)* comparisons of multiple methods in empirical settings.

While each method has been evaluated individually with simulations, comparison of the methods under a common simulation has not been performed. Such a simulation would begin by placing a known number of animals moving about a virtual landscape. Multiple animal movement processes (e.g., random walk versus Brownian motion) should be evaluated, and multiple "species" should be simulated that show different movement speeds, home range sizes, and grouping behaviors (Quaglietta & Porto 2019). Moreover, the landscape should incorporate some level of environmental heterogeneity—at least, binary habitat and nonhabitat classes—that influences the

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position of simulated animals (Sciaini et al. 2018). Next, cameras should be simulated under different sampling scenarios (e.g., systematic or random), varying the number and spacing of cameras. Contacts between animals and the cameras would provide data with which to evaluate the models. Ideally, such simulations could be encapsulated in a program (e.g., an R package), which would *1)* accommodate new methods as they emerge and *2)* provide practitioners with the ability to compare the performance of methods under conditions relevant to their studies.

Simulations are helpful but must be accompanied by rigorous empirical testing to establish the validity of unmarked abundance estimates in real systems. Though possible to simulate multiple types of animal movement in virtual landscapes, it is difficult to know which, if any, of the types accurately represent animals moving through real landscapes. Several empirical comparisons of unmarked methods already exist and provide insight to the performance of multiple methods in common systems (Doran-Myers 2018; Burgar et al. 2018; Ruprecht et al. 2020). However, we suggest that further empirical comparisons would be valuable for identifying systems or conditions where abundance estimates from different methods diverge. Because some of the unmarked methods have incompatible sampling requirements, researchers should select two or more methods with similar sampling requirements and compare the abundance estimates that each provides. Such efforts should be paired with simulations that are fine-tuned to the focal system and species to evaluate the veracity of the simulations described above.

Conclusion

Camera trapping has transformed biodiversity monitoring and continues to grow in popularity. However, abundance estimation of unmarked populations remains a salient frontier for camera trap studies; few studies (about 5% over the last 5 years) even attempt to estimate absolute abundance of unmarked populations. Several analytical frameworks have been developed to do just

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that, but each faces a unique set of limitations and disadvantages. Ultimately, the analytical approaches are similar in that they face the same challenges and share certain assumptions (e.g., all assume population closure in their basic formulations), but each method addresses the challenges facing density estimation with unique data and sampling requirements. As a result, data collected for one modeling method will likely not be compatible with another. Any given modeling approach addresses challenges by either collecting more information or making more assumptions. Approaches requiring ancillary data directly address the challenges but sacrifice feasibility, as these data are difficult to collect. Conversely, approaches that rely on methodological assumptions require less data but potentially sacrifice accuracy, precision, and applicability to real systems. We urge practitioners to proceed with caution when making inference about the abundance of unmarked populations. First and foremost, we emphasize that practitioners should design studies with careful attention to the life history of the focal species and the size of the study area. When possible, we encourage practitioners to seek opportunities to mark individuals or reframe their objectives to target relative abundance, being cautious to address the implicit assumptions that underlie even the most basic of indices. Regardless of the method that is chosen, we urge practitioners to report the assumptions that are made in their analyses and try to evaluate the consequences of violating them. Looking forward, we suggest simulation studies to validate the methods under common conditions and further empirical comparisons of the methods in real systems. As the analytical frameworks for camera trap data continue to evolve, cameras will become even more vital to conservation decision-making.

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Table 1. Summary of the output, design considerations, data requirements, and assumptions for each method.

		Site-structured Kéry & Royle (2015)	**Unmarked SCR** Chandler & Royle (2013)	**REM** Rowcliff et al. (2008)	**TTE** Moeller et al. (2018)	**STE, IS** Moeller et al. (2018)	**DS** Howe et al. (2017)
Output	Spatial variation in abundance	X	X		X		
	Estimate corresponds to known area		X				
	Estimate corresponds to collective viewshed of cameras and is extrapolated to sampling frame			X	X	X	X
Design	Individuals should not be detected by multiple cameras	X					
	Cameras random relative to animals			X	X	X	X
	Must censor data to include times only when animals are active			X			X
Data	Area of viewshed			X	X	X	X
	Animal movement			X	X		
	Distance to animal						X
	Time-lapse photos					X	
Assumption	Closure	X	X	X	X	X	X
	No false positive detections	X	X	X	X	X	X
	No false negative detections				X	X	
	Independent detections	X	X	X	X	X	X
	Activity centers do not move		X				
	Animals not attracted or repelled to each other		X	X			
	Fewer detections as distance between activity centers and camera increases		X				
	Animals at distance 0 perfectly detected						X
	Animals detected at initial location						X
	Distances measured accurately						X

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Figure captions

Figure 1. The number of peer-reviewed publications using camera traps has increased rapidly over the last decade. However, the number of studies using abundance estimation methods has lagged behind other applications of camera traps. In particular, the number of studies applying unmarked abundance estimation methods has been increasing only over the last five years. The studies were sampled with *(camera trap* OR remote camera*) AND (wildlife OR mammal* OR bird*)* search terms on Web of Science and filtered to include only empirical field studies.

Figure 2. Design and data considerations for the methods covered in this review. In (A), the *effective sampling areas* for individual cameras are functions of animal movement and survey length and therefore unknown. In (B), what we show as the *sampling frame* is the prescribed state-space for the spatial process generating the activity centers of individuals. In (C-E), the effective sampling area of a camera is defined as the camera’s viewshed, and the camera locations are assumed to be representative of the sampling frame. In (D), the clock symbols represent the need for time-lapse photos, and in (E), the ruler symbols represent the need for distances to detected animals to be measured.

Figure 3. Decision tree for recommended practices of abundance estimation of unmarked populations. Knowledge of the study area and the life history of the focal species should be leading considerations when designing a study. If alternative state variables can be used to achieve objectives, practitioners should pursue those. If marking any individuals (either by natural or artificial marks) is an option, practitioners should explore spatial mark-resight models. If using the methods covered in this review to estimate absolute abundance (rather than relative abundance), practitioners should proceed with caution and carefully evaluate the degree to which assumptions are violated.

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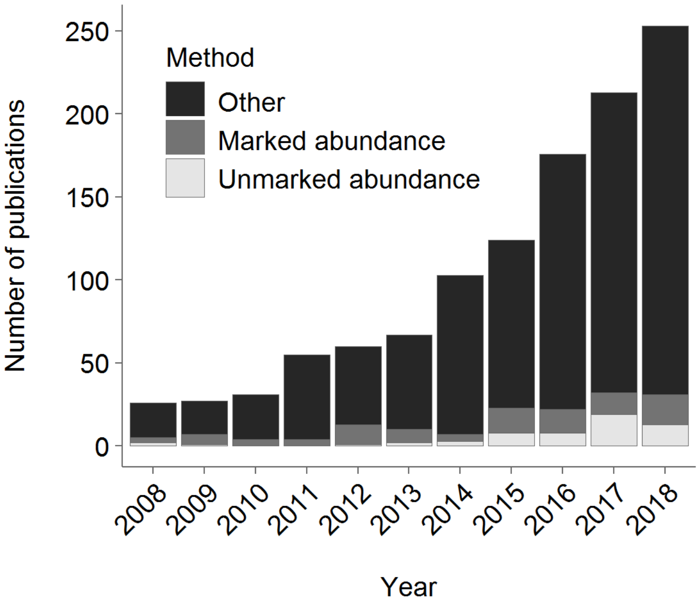
Figures



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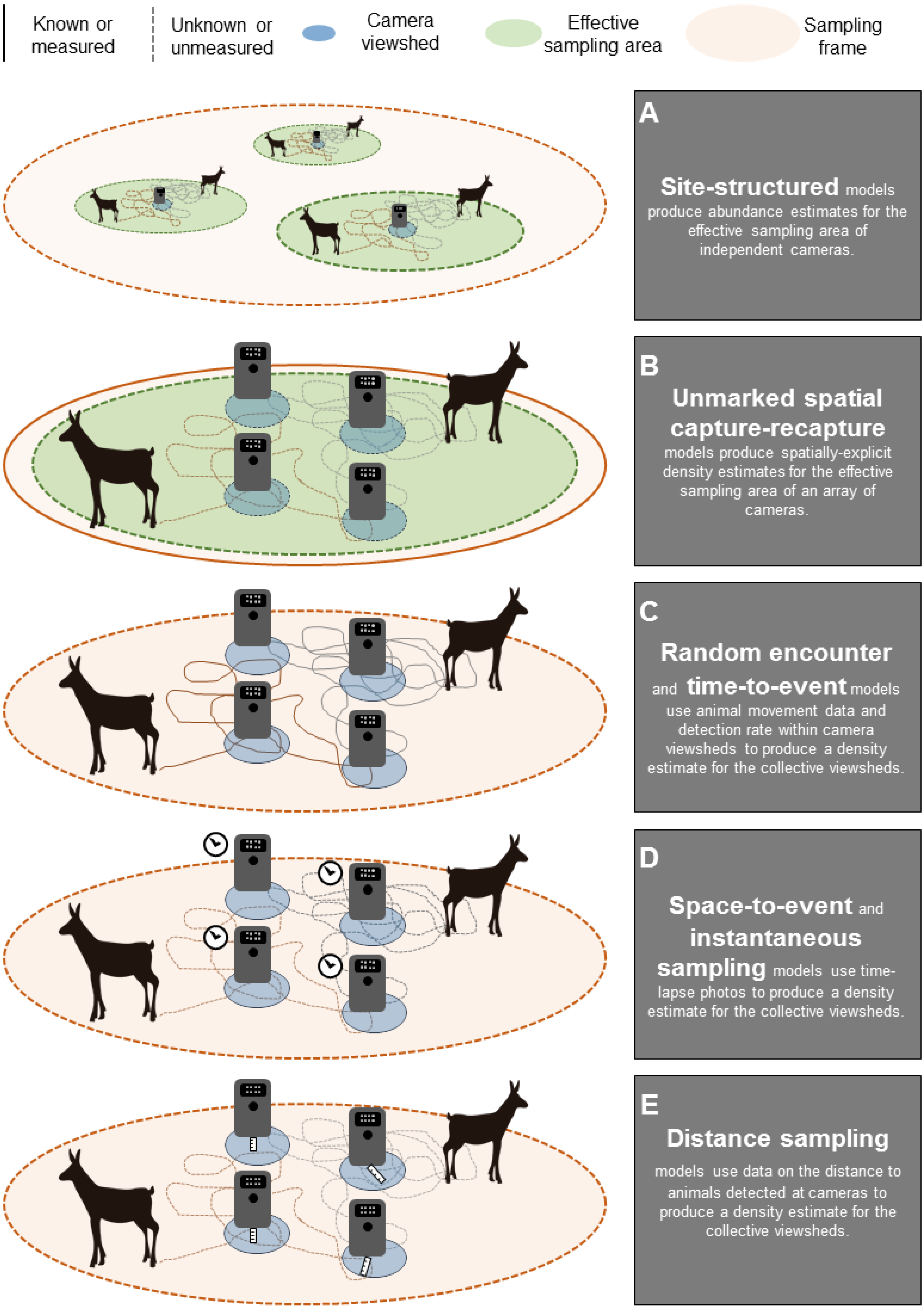

A

Site-structured models produce abundance estimates for the effective sampling area of independent cameras.

B

Unmarked spatial capture-recapture models produce spatially-explicit density estimates for the effective sampling area of an array of cameras.

C

Random encounter and **time-to-event** models use animal movement data and detection rate within camera viewsheds to produce a density estimate for the collective viewsheds.

D

Space-to-event and **instantaneous sampling** models use time-lapse photos to produce a density estimate for the collective viewsheds.

E

Distance sampling models use data on the distance to animals detected at cameras to produce a density estimate for the collective viewsheds.

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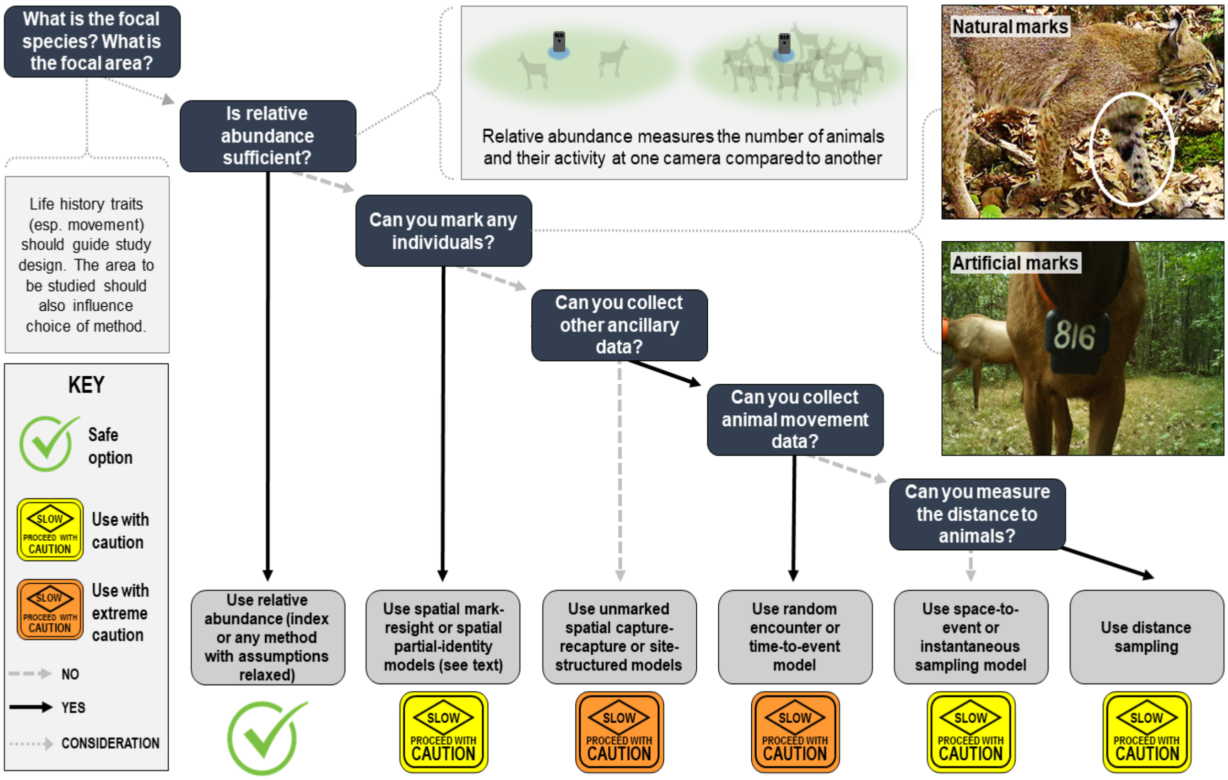

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