Conservation Biology

Review

Abundance estimation of unmarked animals based on camera-trap data

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Abstract: The rapid improvement of camera traps in recent decades has revolutionized biodiversity monitoring. Despite clear applications in conservation science, camera traps have seldom been used to model the abundance of unmarked animal populations. We sought to summarize the challenges facing abundance estimation of unmarked animals, compile an overview of existing analytical frameworks, and provide guidance for practitioners seeking a suitable method. When a camera records multiple detections of an unmarked animal, one cannot determine whether the images represent multiple mobile individuals or a single individual repeatedly entering the camera viewshed. Furthermore, animal movement obfuscates a clear definition of the sampling area and, as a result, the area to which an abundance estimate corresponds. Recognizing these challenges, we identified 6 analytical approaches and reviewed 927 camera-trap studies published from 2014 to 2019 to assess the use and prevalence of each method. Only about 5% of the studies used any of the abundance-estimation methods we identified. Most of these studies estimated local abundance or covariate relationships rather than predicting abundance or density over broader areas. Next, for each analytical approach, we compiled the data requirements, assumptions, advantages, and disadvantages to help practitioners navigate the landscape of abundance estimation methods. When seeking an appropriate method, practitioners should evaluate the life history of the focal taxa, carefully define the area of the sampling frame, and consider what types of data collection are possible. The challenge of estimating abundance of unmarked animal populations persists; although multiple methods exist, no one method is optimal for camera-trap data under all circumstances. 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.

Keywords: biodiversity monitoring, hierarchical modeling, noninvasive methods, population density, population modeling, prediction, species distribution models

Estimación de la Abundancia de Animales No Marcados con Base en Datos de Cámaras Trampa

Resumen: La rápida mejoría de las cámaras trampa en las décadas recientes ha revolucionado el monitoreo de la biodiversidad. A pesar de su clara aplicación en las ciencias de la conservación, las cámaras trampa han sido utilizadas pocas veces para modelar la abundancia de las poblaciones de animales no marcados. Buscamos resumir los retos que enfrenta la estimación de la abundancia de animales no marcados, compilar una perspectiva general de los marcos analíticos de trabajo existentes y proporcionar una guía para aquellos practicantes que buscan un método adecuado. Cuando una cámara registra múltiples detecciones de animales no marcados, no se puede determinar si las imágenes representan a diferentes individuos en movimiento o a un solo individuo que entra repetidamente a la zona de visión de la cámara. Sumado a esto, el movimiento animal ofusca una definición clara del área de muestreo y, como resultado, del área a la cual corresponde un estimado de abundancia. Después de reconocer estos retos, identificamos seis estrategias analíticas y revisamos 927 estudios con cámaras trampa publicados entre 2014 y 2019 para evaluar el uso y la prevalencia de cada método. Solamente en el 5% de los estudios se usó cualquiera de los métodos de estimación de abundancia que identificamos. La mayoría de estos estudios estimaron la abundancia local o las relaciones de covarianza en lugar de predecir la abundancia o la

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densidad a lo largo de áreas más amplias. Después, para cada estrategia analítica, recopilamos los requerimientos de datos, suposiciones, ventajas y desventajas para ayudar a los practicantes a navegar el paisaje de los métodos de estimación de abundancia. Cuando los practicantes busquen un método apropiado deberán evaluar la historia de vida del taxón focal, definir cuidadosamente el área del marco de muestreo y considerar cuáles tipos de recolección de datos son posibles. El reto de estimar la abundancia de poblaciones de animales no marcados persiste; aunque existan muchos métodos, no hay método único óptimo para los datos de las cámaras trampa que cumpla con todas las circunstancias. Mientras los marcos analíticos de trabajo sigan evolucionando y la estimación de la abundancia de animales no marcados sea cada vez más común, las cámaras trampa serán todavía más importantes para informar la toma de decisiones de conservación.

Palabras Clave: densidad de población, métodos no invasivos, modelado jerárquico, modelado poblacional, modelos de distribución de especies, monitoreo de la biodiversidad, predicción

摘要: 近几十年来红外相机陷阱技术的快速发展已经彻底改变了生物多样性监测的现状。尽管红外相机陷阱法在动物保护科学中有明确的应用, 但它很少被用来模拟无标记动物的种群数量。本研究旨在总结无标记动物的丰度估计所面临的挑战, 总结现有的分析框架并为寻求合适方法的实践者提供指导意见。当红外相机多次记录到无标记的动物时, 人们无法确定这些图像代表的是多个个体还是一个重复进入相机拍摄范围的个体。此外, 动物的运动导致不能清晰地划定采样区域, 因此也模糊了所对应区域的丰度估计。面对这些挑战, 我们确定了六种分析方法, 并综述了 2014 年至 2019 年发表的 927 项红外相机陷阱研究, 以评估每种方法的使用情况和流行程度。结果发现, 只有约 5% 的研究使用了至少一种我们确定的丰度估计方法。这些研究大多是估计局部丰度或协变量关系, 而不是预测更大范围内的动物丰度或密度。接下来, 我们总结了每种分析方法的数据需求、假设、优点和缺点, 以帮助实践者了解丰度估计方法的总体情况。实践者在寻找合适的方法时, 应评估研究所关注类群的生活史, 谨慎地确定采样范围, 并考虑可能收集到的数据类型。无标记动物的种群数量估计仍面临挑战, 虽然已存在多种方法, 但没有一种方法对于所有红外相机陷阱数据都是最优的。随着分析框架的不断发展和对无标记动物数量估计变得越来越普遍, 红外相机陷阱法在为指导保护决策中也将更加重要。【**翻译: 胡怡思; 审校: 聂永刚**】

关键词: 生物多样性监测, 层级模型, 种群密度, 种群建模, 预测, 无损伤方法, 物种分布模型

Introduction

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 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 estimated abundance focused 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 had 3 goals with this review: describe the challenges facing abundance estimation of unmarked populations; review current methods for estimating animal abundance with data from camera traps, with a focus on the data requirements, assumptions, advantages, and disadvantages of each method; and highlight considerations for practitioners designing studies to model the abundance of unmarked animals with camera-trap data.

Challenges of Individual Identity, Animal Movement, and Space

Many traditional methods of abundance estimation 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 disentangle the multiple-mobile versus single-sedentary problem while correcting for animals present but not detected.

Abundance requires reference to space to be meaningful, either by reporting the area to which an abundance estimate corresponds (e.g., we estimated an

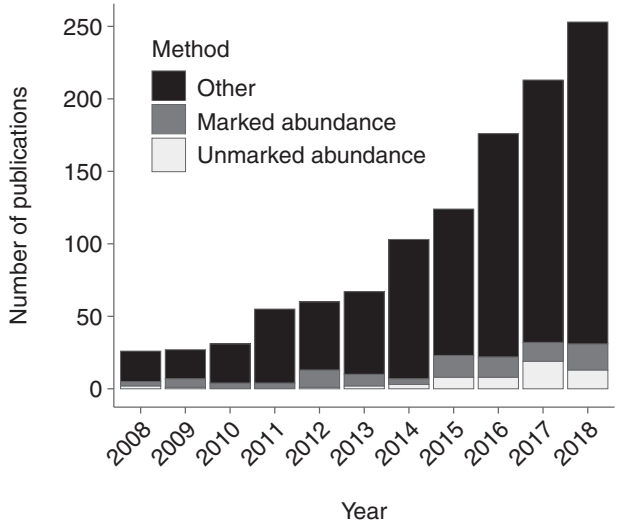

Figure 1. Number of peer-reviewed publications for which researchers used camera traps to estimate abundance of unmarked animals (light gray) and to estimate abundance of marked animals (medium gray) relative to all other applications of camera traps (black) from 2008 to 2018.

abundance of 10 squirrels in the 5 km^2 reserve) or by estimating population density (e.g., we estimated a density of 2 squirrels/km^2). However, the effective sampling area of a camera—the area a camera samples given how far detected animals move—is generally unknown because animal movement information is usually unknown (Fig. 2). Consequently, the sampling frame—the broader study area about which one wishes 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 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 the area within which animals can be detected by a camera's motion sensor (detection viewshed) or the total area photographed by a camera (total viewshed).

Methods to Estimate Abundance or Density from Camera-Trap Data

Recent Use of 6 Analytical Frameworks

We reviewed the data requirements, assumptions, sampling requirements, extensions, advantages, and disadvantages of the following methods: site-structured models (including *N*-mixture and Royle–Nichols [RN] models), unmarked spatial capture-recapture, random encounter model, time-to-event model, 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.

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 from 2014 to 2019. We used 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 1150 papers. We omitted studies that did not use camera traps, were exclusively review articles, or were purely methodological (e.g., software development). We reviewed the 927 papers that satisfied these criteria and noted whether the study used any of the methods we reviewed and whether the population studied was unmarked. For studies that used the methods we reviewed, we noted the inferential goal of the study (estimating abundance or density or both, quantifying covariate relationships, predicting abundance or density or both at unsampled locations). Furthermore, we evaluated whether each study listed or evaluated model assumptions. We classified a study as having evaluated assumptions if it deployed cameras in such a way to satisfy model assumptions, modified analyses to test or account for possible assumption violation, or discussed possible assumption violation and implications for interpretation.

Fifty-one studies (5.5%) used the methods 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 were the default analytical option for many practitioners (Sollmann et al. 2013*b*; Burton et al. 2015). Of the 51 studies in which the methods we identified were used, 22 (43%) used the RN model, 14 (27%) the random encounter model, 13 (25%) *N*-mixture models, and 4 (8%) unmarked spatial capture-recapture. The former three methods were the earliest to appear in the literature (2003, 2008, and 2004, respectively); thus, their prevalence in our sample is unsurprising. We did not capture any studies that used distance-sampling methods, 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, and only 3 (6%) predicted abundance over a broader area. Finally,

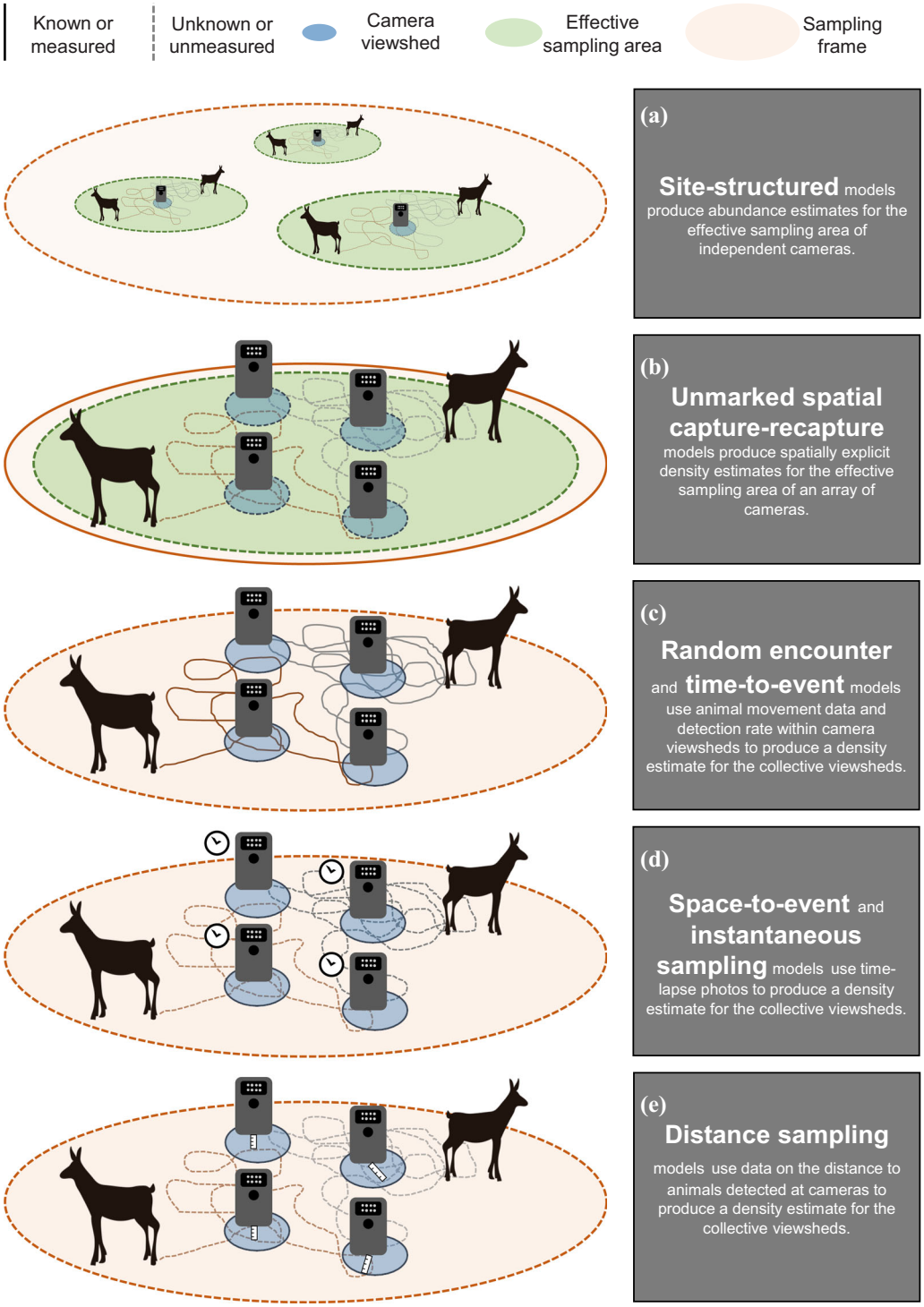

Figure 2. Design and data considerations for the methods to estimate abundance of unmarked animals based on camera traps. In (a) effective sampling areas for individual cameras are functions of animal movement and survey length and therefore unknown. In (c–e) the effective sampling area of a camera is defined as the camera's viewshed, and camera locations are assumed representative of the sampling frame. In (d) the clocks represent the need for time-lapse photos, and in (e) the rulers represent the need for distance measurements to detected animal.

Table 1. Summary of the output, design considerations, data requirements, and assumptions for 6 methods to estimate abundance of unmarked animal populations based on camera-trap data.*.

		Site structured *Kéry & Royle 2015*	***USCR*** *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 to or repelled by 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

**Abbreviations: USCR, unmarked spatial capture-recapture; REM, random encounter model; TTE, time-to-event model; STE, space-to-event model; IS, instantaneous sampling model; DS, distance sampling.*

28 (55%) of the studies listed model assumptions, and 23 (45%) evaluated assumption violations in some way.

Site-Structured Models

Site-structured models use replicated survey periods at independent locations (i.e., 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 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), whereas *N*-mixture models (Royle 2004) require count data (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); equal detection probability for all individuals; no false-positive detections (i.e., misidentifications or double counting of individuals); and independent detections of individual animals at a camera (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 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). The *N*-mixture model 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 1s 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 cause biased abundance estimates that cannot 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). Unmarked spatial capture-recapture estimates density by modeling the number and distribution of animal activity centers as a realization of a spatial point process within the state space, an explicit region of inference defined within the model (Fig. 2b) (Royle et al. 2014). These models require 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).

With USCR, one assumes that activity centers of individuals do not move, that 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, although the counts at individual cameras are assumed to be independent from one sampling occasion to the next (Table 1 & Fig. 2b) (Chandler & Royle 2013).

The ability to estimate abundance within a clearly defined area is an advantage of USCR. Although the basic formulation of USCR does not accommodate spatial variation in density, Evans and Rittenhouse (2018) extended USCR to quantify spatial variation in density as a function of covariates, although further research is warranted to corroborate the robustness of such an approach. A disadvantage of USCR is that it is 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 that 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 estimate density within the collective detection viewsheds of a camera array (Fig. 2c). The REM 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). The model assumes population closure of the sampling frame and that individual animals move independently of one another; for species that travel in groups, 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 nonrandom camera placement relative to animals, leads to biased estimates. For example, Cusack et al. (2015) used the REM to estimate African lion (*Panthera leo*) density and found that cameras placed beneath shade trees (which attracted lions) led to biased estimates compared with 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. Instead, the model relies on 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). The REST model accommodates 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 Model (TTE)

The TTE 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 on restrictive assumptions. In particular, perfect detection is rarely a valid assumption for motion-triggered cameras. The TTE also relies heavily on the assumption that animals are distributed according to a Poisson process; any consequences of violating this fundamental assumption have yet to be demonstrated. Although the density estimate clearly corresponds to the collective viewsheds of individual cameras, inference about the sampling frame requires arbitrary definition of 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 (*Cervus canadensis*) herd. In real-world applications, practitioners seldom have GPS-marked animals to define a biologically meaningful sampling frame. 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) suggest the TTE is negatively biased, particularly for slow-moving species.

Space-to-Event Model (STE) and Instantaneous Sampling Model (IS)

The STE model is an extension of the TTE model in which time-lapse photos are used. Cameras must be programed to take photos at predefined times, regardless of whether an animal is present (Fig. 2d). The IS is an 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 on 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 robust to some variation in movement rate and population density (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, although the density estimate clearly corresponds to the collective viewsheds of cameras, making inference about the abundance of the sampling frame relies heavily on 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).

With DS, one assumes that detectors are randomly located relative to animals, animals at distance 0 are perfectly detected, animals are detected at their initial location, distances are measured accurately, and 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), although making inference about the sampling frame requires strong assumptions about sampling design. Distance sampling has the disadvantage of requiring data that may be difficult to collect (viewshed, distances). 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 compiled a series of considerations to guide practitioners to the method most appropriate for their application (Fig. 3).

Defining the Focal Species

Although 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 time frame 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

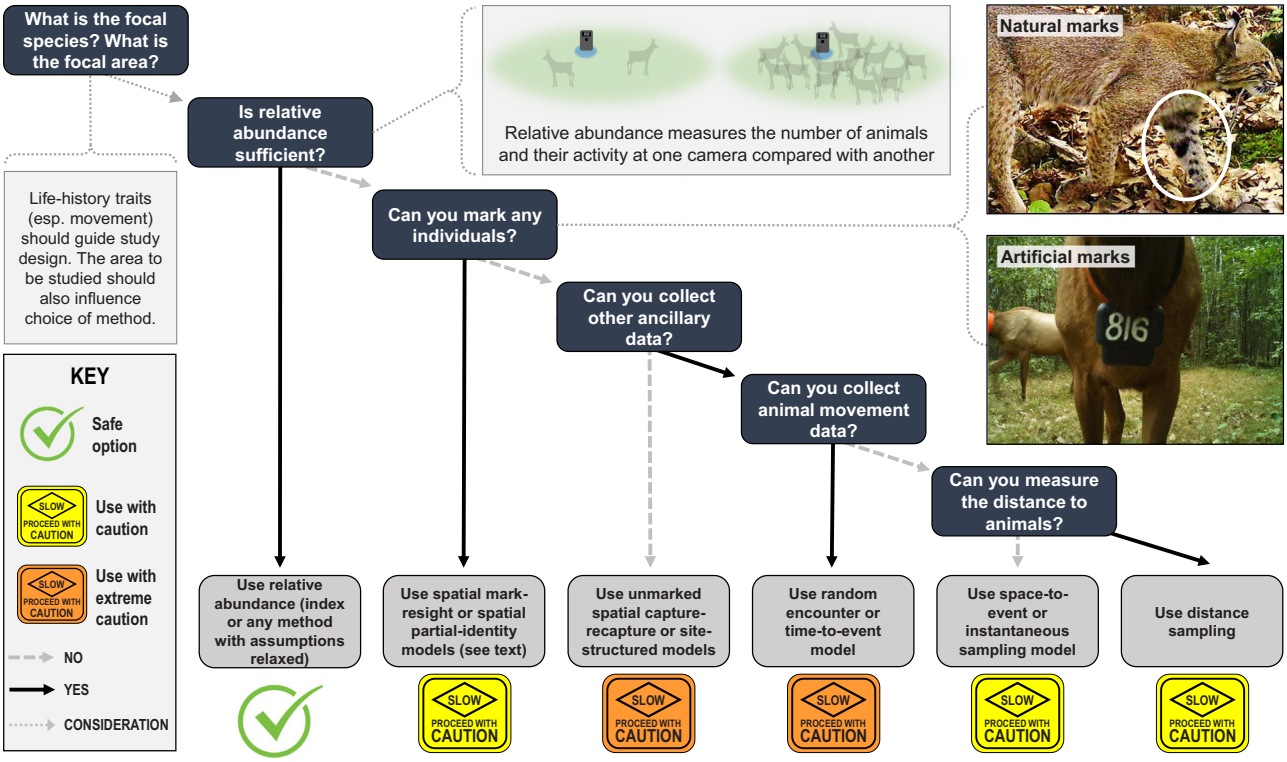

Figure 3. Decision tree for recommended practices of abundance estimation of unmarked populations.

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 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 cameras to 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, 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).

Defining 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 because cameras can be placed at distances greater than the distances moved by individual animals. Practitioners should also consider whether 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).

Sufficiency of Relative Abundance

Given the pitfalls of abundance estimation, researchers should evaluate their objectives to determine whether 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, if relative abundance of an animal is highest in prairies with low amounts of woody vegetation, then 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., number of detection events/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 because they confound abundance and animal movement (Broadley et al. 2019). As such, abundance indices based on detection rate are premised on strong assumptions that movement behavior does not change over space or time (Sollmann et al. 2013*b*; 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. 2013*b*). 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 (Sollmann et al. 2013*b*; 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).

Marking Individuals

Abundance estimation methods that draw on 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 (e.g., 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). 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. 2013*a*; Zipkin & Saunders 2018).

Collection of Ancillary Data

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 for use in 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 and the time-to-event models. Barring intensive behavioral observations or movement data gleaned from the literature (Rowcliffe et al. 2008), animal movement data requires placing radio or GPS tags 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 models. 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.

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 be

trusted to provide accurate abundance estimates and under what conditions? We therefore suggest a set of simulation studies to evaluate the performance methods under common conditions and comparisons of multiple methods in empirical settings.

Although 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 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) that would accommodate new methods as they emerge and 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. Although it is 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 exist and provide insight into 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 researchers (about 5% over the last 5 years) even attempted to estimate absolute abundance of unmarked populations. Several analytical frameworks have been developed to do just that, but each has a unique set of limitations and disadvantages. Ultimately, the analytical approaches face the same challenges and share certain assumptions (e.g., all assume population closure in their basic formulations), but each method addresses the problems of density estimation with unique data and sampling requirements. As a result, data collected for one modeling method will likely not be compatible with another. In general, a given framework addresses the challenges by either collecting more information or making more assumptions. Ancillary data directly address the challenges but can be difficult to collect. Conversely, approaches that rely on 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 chosen, we urge practitioners to report the assumptions that are made in their analyses and try to evaluate the consequences of violating them. We call for 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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