

A gentle introduction to camera-trap data analysis

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Abstract

Camera traps are increasingly used to study wildlife ecology and inform conservation, but valid inference depends on appropriate data analysis. This article introduces the most common analytical approaches for camera-trap data. Camera traps are generally used as point-based sampling devices, and many analytical methods require spatial independence of camera-trap stations and temporal independence of subsequent records. Photographic rates of species should be interpreted with care, because they confound abundance/use with detectability. Occupancy models estimate species occurrence while accounting for imperfect detection and can reveal species–habitat associations. Capture–recapture models estimate abundance and detection probability from individual detection/nondetection data and are applicable to camera-trap data for individually recognizable species. Spatial capture–recapture extends this framework by accounting for animal movement and location relative to the trap array. This is particularly useful for the often wide-ranging species typically studied with camera traps and presents possibilities of modelling spatial population processes. Several methods have been developed to estimate abundance for species that cannot be individually identified; they all heavily rely on model assumptions. Finally, time stamps on camera-trap records can be used to describe activity patterns and temporal interactions between species. Considering the usefulness of camera trapping, we expect ongoing development of analytical approaches for camera-trap data.

Résumé

Les pièges photographiques sont de plus en plus utilisés pour étudier l'écologie de la faune sauvage et renseigner la conservation, mais la validité des conclusions dépend d'une analyse appropriée. Cet article présente les approches analytiques les plus fréquentes pour les données de pièges photographiques. Ceux-ci sont en général utilisés comme des appareils d'échantillonnage basés en un point, et de nombreuses méthodes d'analyse exigent une indépendance spatiale de l'emplacement des pièges photographiques et une indépendance temporelle des rapports qui suivent. Les taux photographiques des espèces doivent être interprétés avec prudence parce qu'ils confondent abondance/présence avec détectabilité. Les modèles d'occupation estiment l'occurrence d'une espèce tout en tenant compte d'une détection imparfaite et ils peuvent révéler des associations espèce-habitat. Les modèles par capture-recapture estiment l'abondance et la probabilité de détection d'une espèce pour des données individuelles de détection/nondétection et ils sont applicables aux données des pièges photographiques pour des espèces reconnaissables.

individuellement. La capture-recapture spatiale élargit ce cadre en prenant en compte le déplacement d'un animal et sa situation par rapport à l'ensemble des pièges. Ceci est particulièrement utile pour les espèces qui font souvent de grands déplacements et qui sont habituellement étudiées au moyen de pièges photographiques et cela offre des possibilités de processus de modélisation spatiale de populations. Plusieurs méthodes ont été développées pour estimer l'abondance d'espèces qui ne peuvent pas être identifiées individuellement ; elles dépendent toutes beaucoup des hypothèses du modèle. Enfin, l'horodatage sur les enregistrements des pièges photographiques peut servir pour décrire le schéma des activités et les interactions temporelles entre espèces. Vu l'utilité des pièges photographiques, nous nous attendons à un développement constant des approches analytiques pour les données qu'ils fournissent.

KEYWORDS

abundance, activity pattern, capture, data analysis, occupancy, photographic rate, recapture

1 | INTRODUCTION

Camera traps have revolutionized our ability to survey elusive and rare mammals and hold great promise to advance ecological understanding and inform conservation of these species. But as for any survey method, the validity of the inference we draw from camera-trap data depends on proper study design and use of appropriate analytical techniques. This paper is intended to introduce the most common analytical approaches for camera-trap data, including the study of species occurrence, richness, abundance and other demographic parameters, as well as activity patterns. It is not a comprehensive review of any one of these topics. Rather, I aim to present the objectives, assumptions and resulting study design considerations of these commonly used analytical tools, and discuss their limitations. The paper also provides references to the primary literature for more advanced topics and details that are beyond its scope.

2 | GENERAL CONSIDERATIONS

Most analytical approaches for camera-trapping data share terminology and concepts. In many applications, a single camera trap is considered a sampling unit in space and is often referred to as a camera-trap station. Here, a camera trap is a point-based detector—a detector that refers to a point in space, rather than an area. This has implications for the interpretation of parameters (see Occupancy and *N*-mixture models, below). Some approaches, such as capture–recapture for individually recognizable species, customarily use two cameras facing each other at each station, to capture both flanks of a passing individual (Karanth & Nichols, 1998). In those cases, the station, rather than the camera, becomes the sampling unit. Some applications define area-based sampling units (grid cells, habitat fragments) and deploy multiple camera traps within that sampling unit

(e.g., Michalski & Peres, 2007), but I will focus on the more common use of camera traps as point-based sampling devices.

Many analytical approaches such as occupancy models require that sampling units are spatially independent of each other, meaning that the observation in one location does not influence what we observe in a nearby location. A simple example of lack of spatial independence is an individual being detected at multiple stations. Therefore, a rule of thumb to approximate spatial independence is to space stations at least approximately one home range diameter of the target species apart from each other. Lack of spatial independence can lead to biased estimates of covariate associations (e.g., Lichstein, Simons, Shriver, & Franzreb, 2002). There are analytical approaches that can account for a lack of spatial independence (e.g., conditional autoregressive models, Besag, York, & Mollié, 1991), but these are beyond the scope of this article. Conversely, spatial capture–recapture requires the same individual to be detected at multiple stations (Royle, Chandler, Sollmann, & Gardner, 2014), and conventional capture–recapture works better when an individual is exposed to multiple traps (Otis, Burnham, & White, 1978). Whether we need spatially independent detectors depends on the analytical approach, and what constitutes spatial independence depends on the focal species. These are important considerations, especially when designing multi-species or multi-purpose studies.

Similarly, many analytical approaches assume that subsequent detections at the same station are temporally independent. To that end, multiple nonindependent pictures (i.e., pictures taken within a short time interval) are condensed into a single independent detection. Without a detailed understanding of activity and movement patterns of the target species, it is difficult to determine an ecologically justified threshold for temporal independence. Some situations are simple. Many camera-trap models take a series of pictures when triggered—these obviously refer to the same event of an animal

passing the camera trap and are thus not independent, constituting a single detection. Similarly, if an individual lingers in front of a camera trap, multiple pictures are not independent, as they represent a single visit by that individual to the station. Problems arise in intermediate situations, when some time passes between subsequent pictures, and we cannot determine whether these pictures represent distinct individuals. Researchers have used different thresholds, typically 30 min (e.g., O'Brien, Kinnaird, & Wibisono, 2003) to an hour (Bahaa-el-din et al., 2016); some researchers have argued that multiple pictures within the same day may not represent independent detections (Royle, Nichols, Karanth, & Gopalaswamy, 2009). In most cases, this threshold is determined subjectively, based on the best available knowledge of the species under study. But it can also be determined based on the temporal autocorrelation (Kays & Parsons, 2014) or analysis of time intervals (Yasuda, 2004) of subsequent pictures.

3 | PHOTOGRAPHIC RATES

An intuitive output from a camera-trap survey is the number of (independent) records of a given species at a sampling location (possibly during a particular time interval, e.g., an ecological season). Dividing the number of records by the sampling effort at that location provides a photographic rate. This quantity is sometimes interpreted as a relative abundance index (RAI, O'Brien et al., 2003). Unfortunately, photographic rates are influenced not only by a species' abundance, but also by its movement patterns, and by camera-trap set-up or habitat, to name just a few factors (Sollmann, Mohamed, Samejima, & Wilting, 2013). Without additional information, we cannot disentangle the effects of these confounding factors from the effects of abundance. Thus, when we compare RAIs across study areas or species, we do not know whether differences are in fact due to differences in abundance or due to differences in any of these other factors. Because of this fundamental flaw, RAIs are not discussed any further here (for a detailed discussion of abundances indices in general, see, e.g., Williams, Nichols, & Conroy, 2002, Chapter 12).

Rather than an index of abundance, photographic rates should be interpreted as an index of activity, where activity of a species at a site can increase because more individuals use that site and/or because individuals use that site more often. In this context, photographic rates can be analysed using generalized linear (mixed) models (see, e.g., Gelman & Hill, 2006, for a thorough introduction to this broad class of models). Fundamentally, GL(M)Ms estimate relationships between predictor and response variables. In the present context, the response variable is the photographic rate, and we can use GL(M)Ms to investigate whether covariates measured at each camera trap (or over time) explain variation in photographic rates (e.g., Foster, Harmsen, & Doncaster, 2010). Covariate associations must be interpreted with care because they can represent both ecological and sampling processes. For example, we could observe higher photographic rates in forested areas compared to grassland because the species under study uses forested areas more frequently (i.e., the

association with forested habitat represents an ecological process), but we could also observe higher rates in forested areas because in dense vegetation, it is easier to target game paths and other features along which animals are likely to move, thus increasing our chances of recording them (i.e., the association with forested habitat represents a sampling process).

4 | OCCUPANCY

Camera traps are a prime tool to study the occurrence of elusive species. Verifying a species' presence is (conceptually) simple—if we record it, we know it is there. On the other hand, failure to detect a species does not prove its absence, because we cannot rule out the possibility that it is indeed present, but we failed to observe it—maybe because it occurs at very low densities or because of insufficient sampling effort. Occupancy models are concerned with describing patterns of species occurrence and can thus be considered a form of species distribution model. But rather than considering only sites where the species was detected as “occupied” (also referred to as “naïve occupancy”), these models account for the fact that a species may be present but missed by our sampling efforts (MacKenzie et al., 2002, 2006). In other words, occupancy models account for imperfect species detection. To do so, these models require sampling multiple sites multiple times. Repeated visits to a site are called “occasions,” and for each site on each occasion, we obtain an observation of 1 if the species was observed or 0 if it was not observed. Data from occupancy surveys thus comprise a site-by-occasion matrix with binary detection/nondetection data. The ability to estimate species detection probability comes from the repeated visits: If the species is observed at a given site on at least one occasion, we know it is present (i.e., the site is occupied), and we can conclude that not observing the species at that site on another occasion is due to nondetection, not species absence. In addition to detection probability, occupancy models estimate occupancy probability ψ , the probability that the focal species occurs at a site. Occupancy probability can be modelled as a function of site-specific covariates (e.g., habitat, human disturbance) to make inference about conditions that favour a species' occurrence. Similarly, detection probability can be modelled as a function of site (e.g., camera location on or off road) and occasion-specific covariates (e.g., weather, temperature) thought to impact how likely a species is detected when present. Occupancy models require that the true occupancy status of a site—whether a site is occupied or not—does not change over the course of our study. Violation of this “closure” assumption can lead to positive bias in occupancy estimates. What survey duration is appropriate to approximate closure depends on the species and system under study; for example, where species occurrence tracks the availability of seasonal resources, an occupancy survey should be constrained to a single season. Other than closure, occupancy models assume independence of observations, both across sites and occasions.

Because camera trapping is a continuous form of sampling, applying occupancy modelling to camera-trapping data requires subdividing the survey into discrete intervals representing the occasions.

Assigning occasions is somewhat arbitrary but should be guided by a few general principles: (a) Avoid having too many occasions with 0 observations (usually very short occasions). Many 0s in the detection matrix will lead to very low estimates of detection probability, which can lead to numerical issues when fitting models. (b) At the same time, avoid losing a lot of information. When condensing data into too few, long occasions, many photographic records of a species at a site will be subsumed into a single entry of “1,” reducing the amount of information that goes into estimating detection probability. (c) Keep occasion length constant. The probability of detecting a species increases with increasing occasion length. If occasion lengths (or effort within an occasion) differ, you may need to account for that in your model, by including occasion length (or effort) as a covariate on detection. (d) Finally, if you study a territorial, low-density and wide-ranging species, consider that the presence of a single individual may determine whether your camera-trap station is occupied or not. As this individual moves about its home range, it may temporarily not be in the vicinity of the camera trap, thus becoming unavailable to be detected. This phenomenon is called temporary emigration (Nichols et al., 2008) and can lead to underestimating detection probability and, consequently, to overestimating occupancy probability. Choosing occasions that are long enough for the individual to have a good chance to be available for detection at some point during the occasion can alleviate some of the problems introduced by animal movement. Appropriate occasion length depends on your data set and focal species. How many sites should be sampled over how many occasions depends on a variety of factors including the species' detection probability and whether the species is rare or common. MacKenzie and Royle (2005) provide general guidelines for allocating effort between sampling more sites or over more occasions.

The difficulties introduced by animal movement hint at a general challenge when applying occupancy models to camera-trap data: Occupancy models were developed for application with discrete habitat patches (e.g., ponds, forest fragments), and in that context, occupancy probability has a clear interpretation as the probability that a patch is occupied by the species of interest. Camera trapping, on the other hand, represents point-based sampling in continuous habitats; occurrence of a wide-ranging species at a one-dimensional point in space is not as easy to interpret. Because animal movement can temporarily lead to absence of the species at a station, estimates of occupancy probability from point-based sampling methods are usually interpreted as probability of use, that is, the probability that a site is used at least once during the survey (MacKenzie & Royle, 2005). Alternatively, studies have ascribed areas to camera-trap stations, often based on known average home range; for example, if a species has an average home range of 5 km², one could assume that occurrence of a species at a camera trap implies occurrence in a 5-km² area around the camera trap. This approach implies the strong assumption that a single point in space provides conclusive information about an area on the scale of multiple square kilometres. The true area sampled by a camera trap is difficult to determine. Because of that, Efford and Dawson (2012) argue that occupancy estimates from point-based surveys in continuous habitat are confounded with density and home

range size and may therefore not be readily comparable across surveys or species. On the other hand, based on simulations and empirical data, Steenweg, Hebblewhite, Whittington, Lukacs, and McKelvey (2018) suggested that camera-trap-based estimates of occupancy can be comparable among species with very different spatial ecology. Both papers provide a thorough overview of the importance of spatial and temporal sampling scale in camera-trap-based occupancy modelling.

Monitoring occupancy has been proposed as an alternative to monitoring abundance (MacKenzie & Nichols, 2004), mostly because occupancy data are easier to obtain across large spatial scales than data necessary for abundance estimation (see Capture–recapture below, and Karanth et al., 2011, for an example). Though an ecologically meaningful quantity in its own right, occupancy should not be misinterpreted as an index of abundance (Efford & Dawson, 2012; MacKenzie & Royle, 2005) as its relationship with abundance depends on multiple factors, including survey duration and animal density (Steenweg et al., 2018), as well as home range size and sampling design.

Basic single-season, single-species occupancy models have been extended in many ways. A few extensions commonly applied to camera-trap data include the following: *Two-species occupancy models*, also referred to as co-occurrence models, allow investigation of patterns of co-occurrence and avoidance (MacKenzie, Bailey, & Nichols, 2004). They have been applied to camera-trap data to investigate spatial segregation/overlap between competitor species (e.g., Ramesh, Kalle, & Downs, 2017) as well as predators and their prey (e.g., Farris, Karpany, Ratelolahy, & Kelly, 2014). Recently, these interaction models have been extended to more than two species (Rota et al., 2016). *Community occupancy models* (see also *Species richness* below) jointly model data of multiple species, which allows sharing information across species and thus improves parameter estimates for data-poor species (Dorazio & Royle, 2005). Combined with camera trapping, this approach has been used to investigate spatial patterns in species richness in space (e.g., Burton, Sam, Balangtaa, & Brashares, 2012). *The Royle–Nichols model* (Royle & Nichols, 2003) allows estimation of local abundance (i.e., at a camera trap) from species detection/nondetection data and is discussed further under Abundance estimation without individual identity. *Multi-season or dynamic occupancy models* allow estimation of dynamic parameters such as patch extinction and colonization (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). They can be used to analyse data from camera-trap surveys that are repeated over multiple years or seasons, given that the same sampling locations are maintained over time. Dynamic occupancy models have been used, for example, to investigate changes in occupancy of native and exotic carnivores in Madagascar (e.g., Farris et al., 2017), or seasonal variation in occurrence of forest mammals in Tanzania (Martin, Ndibalema, & Rovero, 2017).

5 | SPECIES RICHNESS

Camera traps simultaneously collect data on a suite of species and are thus a prime tool to estimate species richness. Just as we can fail to detect a single species at a site at which it is present, when

surveying for species richness, we may fail to detect a species in our survey even though it is part of the sampled community. A variety of analytical methods exist to overcome this problem of imperfect species detection in the context of richness estimation. Species accumulation curves (e.g., Gotelli & Colwell, 2001) plot the cumulative number of species detected against survey effort; their asymptote corresponds to species richness, which can be estimated if the data suggest it has not been reached. Alternatively, capture–recapture-type estimators (Chao, 2004), which use detection/nondetection data for all species across survey occasions, can be used to estimate species richness in the study area (e.g., Tobler, Carrillo-Percegueiro, Leite Pitman, Mares, & Powell, 2008).

Camera-trap data consist of species, station and occasion-specific detections, but both accumulation curves and capture–recapture-type estimators ignore the spatial component of the data, thereby losing interesting information on how richness may vary within a study area. Community occupancy models (e.g., Dorazio & Royle, 2005), mentioned in the previous section, make use of this information and allow estimating the number of species present at any given camera-trap station, as well as the total number of species in the study area. The data structure for these models allows for detailed modelling of variation in detection probability (with time, in space, by species), which is important for obtaining unbiased richness estimates.

6 | ABUNDANCE, DENSITY AND DEMOGRAPHIC PARAMETERS

Like species occurrence, determining population size suffers from our imperfect ability to count all animals in a population of interest. Capture–recapture (CR) models have a long tradition in mammalian population ecology (Lincoln, 1930) as the gold standard to estimate demographic parameters such as population size and density, survival or recruitment, while accounting for imperfect individual detection. For species with individual coat patterns, camera traps have revolutionized our ability to collect individual-level detection data noninvasively (e.g., leopards, Chapman & Balme, 2010).

Capture–recapture models can be divided into closed population models, which assume no loss or gain in individuals over the course of the study and focus on estimating abundance and density (Otis et al., 1978), and open population models, which focus on estimating dynamic parameters such as survival and recruitment (Pollock, Nichols, Brownie, & Hines, 1990). Closed population CR models have frequently been applied to camera-trap data of naturally marked species. In these applications, an array of paired camera-trap stations is placed in a manner that increases chances of detecting the target species (e.g., for carnivores, that often means placing cameras along roads and trails) and that leaves no gaps within the array large enough to contain an entire home range. Ideally, each home range contains multiple camera traps, to increase chances of detection. As a rule of thumb, arrays should cover at least 4 times the average home range for appropriate density estimation (Maffei & Noss, 2008; see also below). Further, Otis et al. (1978) suggested a

minimum of 25 recorded individuals to obtain reliable abundance estimates. Cameras are run for a period that is long enough to obtain sufficient captures and recaptures of individuals, yet short enough to approximate a closed population (as before, what constitutes “short enough” depends on the ecology of the focal species). Individuals are identified from photographs, and detection histories are created by first dividing the study period into sampling occasions, then collapsing detection information across the entire array and noting whether or not (1 or 0) an individual was detected during an occasion. Analogous to occupancy modelling, occasions should be defined in a manner that minimizes the loss of recapture information and that reduces the number of 0s in the detection history matrix to increase detection probability and improve the reliability of abundance estimates (Otis et al., 1978).

Adequately modelling the detection process is important in obtaining unbiased abundance estimates, and therefore, fitting CR models often involves exploring different sources of heterogeneity in detection probability. Traditional models include variation with time (i.e., across occasions), a behavioural response to trapping that leads to the first detection having a different probability than subsequent detections (that seems less likely in camera traps than when dealing with baited life traps, but several studies have reported such effects in camera-trap studies, e.g., Wegge, Pokheral, & Jnawali, 2004), and individual variation, either due to measured covariates (sex, age; e.g., Sollmann et al., 2011) or due to unmeasured factors (latent heterogeneity models; e.g., Pledger, 2000). Akaike’s information criterion (AIC, Burnham & Anderson, 2002) can then be used to select the model that best describes the data with the fewest parameters.

The above-described procedure yields an estimate of abundance, but density is frequently a more useful measure to compare populations across study areas, time or species. Species studied with camera traps tend to be highly mobile and are thus bound to use areas beyond the immediate camera-trap array. The difficulty in determining this effective sampled area to estimate density has long been recognized (Bondrup-Nielsen, 1983; Parmenter et al., 2003; Wilson & Anderson, 1985). Measures of movement across the camera array (mean maximum distance moved between detections, for example) have been used to buffer the camera-trap array and determine the effective sampled area, but because there is no consensus on which measure to use, and because width of the chosen buffer directly impacts density estimates, these become arbitrary and not comparable across studies (e.g., Dillon & Kelly, 2007). How much individual home ranges overlap with the camera-trap array also influences how likely individuals are to be detected—a source of heterogeneity in detection probability that cannot be addressed explicitly in traditional capture–recapture.

The framework of spatial capture–recapture (SCR, Efford, 2004; Royle et al., 2014) emerged in response to these challenges. SCR does not collapse detections across the entire camera array but makes use of the information where an individual was detected, to describe how the spatial juxtaposition of individual home ranges with sampling effort affects detection probability. The model assumes that detection probability decreases with increasing distance from an individual’s

activity centre (conceptually, the midpoint of an individual's home range); where we observe an animal on the sampling array provides some (albeit imperfect) information on where that activity centre is located. Further, the model assumes that activity centres are distributed according to a spatial point process; the spatial domain for that process—the area in which activity centres can be located, called the state space—is set so that it includes the activity centres of all individuals that could have been exposed to sampling. Once large enough, increasing the size of the state space does not influence density estimates (contrary to the buffer approach in traditional CR). Density in SCR is clearly defined as the number of activity centres in the state space divided by its area.

The input for an SCR model consists of the spatial encounter histories, showing how many times each individual was detected at each station, and the coordinates of all stations. In addition to density, the model estimates the parameters of the detection function, which describes the decrease in detection with distance to the animal's activity centre. A common choice is the half-normal function, which is defined by the baseline trap encounter rate—the encounter rate at a (hypothetical) camera trap located at an individual's activity centre—and a scale parameter that determines how quickly the encounter rate declines with distance to the activity centre. The scale parameter is related to how far animals typically move (if they move over larger distances, their encounter rates will decline more slowly) and is therefore also sometimes referred to as the movement parameter.

Spatial capture–recapture allows for more flexible study design compared to traditional CR, for two main reasons: First, because SCR explicitly models animal movement, the camera array does not have to cover at least 4 times an average home range; as long as sample size (number of individuals, recaptures) is sufficient, covering an area of approximately one home range is appropriate (Sollmann, Gardner, & Belant, 2012; Tobler & Powell, 2013). That is particularly advantageous when studying wide-ranging mammals. Second, SCR does not have the “no gaps” requirement of traditional CR, so that large areas can be sampled using clusters of camera traps (Efford & Fewster, 2013; Sun, Fuller, & Royle, 2014). SCR requires observations of (at least some) individuals at multiple camera traps to estimate the scale or movement parameter, and camera traps should be spaced accordingly. Finally, because the detection process in SCR can be parameterized in terms of encounter rates (rather than probabilities), there is no need to divide the study period into discrete occasions (unless the goal is to model variation in encounter rates over time), or to reduce observations to a 0/1 format. Instead, SCR works directly with the number of independent records of an individual at a trap. Much like traditional CR, SCR models assume that individuals are detected independently of each other. That assumption is violated for group-living species, where individuals travel together and thus are detected together, and for young individuals who are not observed independent of their parents. It is unclear to what extent violation of this assumption affects density estimates (e.g., Russell et al., 2012).

Similar to regular CR, SCR can accommodate sources of heterogeneity in baseline encounter rate among individuals or across time. But because we consider the detection process at the level of the camera-trap station, we can now also model variation in baseline detection across space (e.g., Sollmann et al., 2011 showed that baseline detection of jaguars was a lot higher at cameras set along roads, as compared to off-road cameras). Considering the benefits SCR offers over traditional CR, it seems the preferable framework for population estimation in camera-trap studies, which predominantly focus on wide-ranging species.

The basic SCR framework can readily be extended to incorporate spatial processes of interest to ecologists: Density can vary across the state space and we can model that variation using environmental covariates (Borchers & Efford, 2008); resource selection functions can be incorporated into SCR models to account for the fact that animals use different habitats with different intensity, leading to a more realistic representation of animal space use (Royle, Chandler, Sun, & Fuller, 2013); instead of using Euclidean distance between activity centres and detectors, models can make use of resistance surfaces to adequately reflect individual movement across the landscape (Sutherland, Fuller, & Royle, 2015). SCR models can also be extended to open populations (e.g., Gardner, Reppucci, Lucherini, & Royle, 2010; see also next paragraph) and resighting surveys of artificially marked individuals (i.e., mark–resight, Sollmann, Gardner, et al., 2013), but these advancements are not yet fully generalized.

Camera-trap-based open population capture–recapture applications remain relatively rare. The variety of modelling approaches and sampling designs for open population models is broad, but the design most applicable to camera trapping is Pollock's robust design (RD, Pollock, 1982). The RD design consists of data collection on two temporal scales. Primary occasions are those across which the population is allowed to change (a year or a season). Dynamic processes such as survival and recruitment happen between primary occasions. Within each primary occasion, a closed population survey is conducted to estimate population size and detection probability. Intervals between subsequent closed population surveys should be long compared to the duration of a closed population survey. This combination of open and closed population sampling and modelling allows for estimation of population size through time, as well as demographic parameters including survival, recruitment and temporary emigration (Pollock et al., 1990), and was spearheaded in camera-trap studies by Karanth, Nichols, Kumar, and Hines, (2006), studying tiger population dynamics.

7 | ABUNDANCE ESTIMATION WITHOUT INDIVIDUAL IDENTITY

The above-described (S)CR approaches require individual identification of animals, which for camera trapping is limited to those species with individual coat patterns (or requires artificial marking of animals). Several methods have been developed that allow estimating population size without individual identification; however, all these methods rely heavily on assumptions made about the data—

assumptions that, in the absence of individual identification, cannot readily be tested. As such, these methods have to be treated with great care. Due to limited space and difficulty of the subject, I will not discuss these methods in detail, but provide a brief overview.

The Royle–Nichols (RN) model (Royle & Nichols, 2003) is an extension to regular occupancy models, built on the notion that the more individuals of a given species occur at a sampling location, the more likely we are to detect the species (or in other words, the more likely we are to detect at least one individual). Detection probability, therefore, carries information about local abundance. The RN model uses this relationship to estimate local abundance (i.e., abundance at a camera-trap location) using regular occupancy-type species detection/nondetection data. Potential issues with this approach include that the true relationship between local abundance and species detection probability is likely more complex (e.g., due to individual variation in detectability) and, specifically for camera trapping, that it is unclear to which area the resulting local abundance estimates refers, hampering ecological interpretation.

Whereas the RN model relies on spatially independent survey locations, Chandler and Royle (2013) developed a model that makes use of spatial correlation in counts across closely spaced detectors to estimate animal density—essentially an SCR model without individual identification. This model is very sensitive to study design. Based on personal (and unpublished) experience, comparing the Chandler and Royle model results to those of a SCR model, the former often fails to provide reasonable density estimates, but see Jiménez et al. (2017) for a successful application to camera-trapping data.

Rowcliffe, Field, Turvey, and Carbone (2008) developed a model for camera-trapping data that assumes individual animals behave like particles in an ideal gas (they move at random) and estimates density as a function of encounter rates between animals and traps and animal movement speed. The model assumes random movement of individuals, requires a random trap set-up relative to animal movement, and knowledge of, or the ability to estimate, movement speed and the amount of time individuals are active. It has been applied to camera-trap data of several mammal species (Cusack et al., 2015; Manzo, Bartolommei, Rowcliffe, & Cozzolino, 2012).

Finally, Howe, Buckland, Després-Einspinner, Kühl, and Matthiopoulos (2017) combined distance sampling with camera trapping to estimate animal density, treating each camera trap as a point transect and using distances of detected individuals from the camera trap to estimate detection probability. The method requires accounting for animals not being available for detection by camera traps during periods of inactivity, and doing so requires careful thought and possibly additional data on animal activity patterns.

8 | ACTIVITY PATTERNS

Among other metadata, camera-trap pictures contain timestamps that can be used to describe activity patterns. Traditionally, activity patterns have been constructed by grouping pictures into discrete time intervals (often, 1-hr intervals) and displaying the frequency of

observations in each interval (e.g., Jácomo, Silveira, & Diniz-Filho, 2004). This approach will often provide a valid picture of a species' activity throughout the day, but it relies on artificial grouping of continuous data, and it ignores that time of day is circular. Addressing these shortcomings, Ridout and Linkie (2009) developed an approach that fits a smooth, circular curve (specifically, a Kernel density function) to the observed time stamps, where peaks in the curve correspond to peaks in animal activity. The approach is frequently used to compare activity patterns, between species, or otherwise defined groups of individuals (e.g., herbivores at sites with and without large predators, Tambling et al., 2015). Here, the degree to which both curves overlap serves as an index for the similarity of the two activity patterns. Ridout and Linkie (2009) present several estimators of overlap, of which one (termed Δ_1) performs well with as few as 25 records of each species.

The degree of overlap is sometimes interpreted as an index for how much two species interact (low overlap = avoidance; high overlap = attraction); that interpretation, however, ignores the fact that species not only have to be active at the same time, but also in the same location to interact. A more detailed investigation of species interactions considers the time intervals between pictures taken at a particular camera trap of members of a species pair, A and B. Harnsen, Foster, Silver, Ostro, and Doncaster (2009), for example, studied top predator avoidance and extracted, for each camera trap, the time that passed after a record of a jaguar until a puma was recorded again (interval AB) and the reverse (interval BA) and compared means of these two types of intervals. If there is avoidance of species A by species B, we would expect AB intervals to be longer, on average, than BA intervals. Karanth et al. (2017) compared measures of AB to random intervals generated under the assumption of no avoidance. And Parsons et al. (2016), looking at predator–prey interactions, calculated avoidance ratios as AB/BA or as the time intervals between records of a prey species with/without the passage of a predator in between (BAB/BB), where ratios >1 indicate avoidance of A by B. When interpreting any of these time intervals and ratios, we must consider that the presence/activity of other species may well influence the results.

9 | OUTLOOK

Camera traps are used to study a variety of ecological and conservation-related topics, and this brief overview of analytical approaches necessarily remains incomplete. For example, camera traps, particularly those with the ability to record videos, also allow studying aspects of animal behaviour (e.g., Caravaggi et al., 2017), many of which necessitate a different set of analytical tools. The flexibility of standard frameworks such as occupancy and (spatial) capture–recapture models has led to the development of a wide variety of model modifications for particular sampling situations. Considering the ever-increasing technological improvements and the usefulness of camera trapping as a tool to study otherwise elusive wildlife, we can expect a parallel development of novel or improved analytical approaches for camera-trap data.

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