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11.0 Appendix A

Table A1. Summary of the <u>assumptions</u> and pros/cons of the different <u>modelling approaches</u> (adapted from Wearn & Glover-Kapfer [2017] and Clarke et al. [2022]).

Objective	<u>Approach</u>	<u>Assumptions</u>	Pros	Cons	References
Species inventory	Species inventory	• No formal <u>assumptions</u> ¹	Maximum flexibility for study design (e.g., <u>camera days per camera location</u> or use of <u>lure</u> ²) ¹	Not reliable estimates for inference ("considered as unfinished, working drafts")¹	¹ Wearn & Glover- Kapfer, 2017
Species richness	Species richness	Cameras are randomly placed Cameras are independent detection probability of different species is equal ("True" species richness estimation involves attempting to correct for "imperfect detection"	 Fundamental to ecological theory and often a key metric used in management¹ Simple to analyze, interpret and communicate¹ Models exist to estimate asymptotic species richness, including unseen species (simple versions of these models - EstimateS and the "vegan" R-packages)¹ 	 Dependent on the scale (as captured in the species-area relationship)¹ All species have equal weight in calculations, and community evenness is disregarded¹ Insensitive to changes in abundance, community structure and community composition¹ 	 2013 MacKenzie et al., 2002 MacKenzie et al., 2006 Lambert, 1992 Mullahy, 1986 McCullagh &
Species diversity	Species diversity	 Cameras are <u>randomly placed</u>¹ Cameras are independent¹ The <u>detection probability</u> of different species remains the same¹ 	 Captures evenness and richness (although some indices only reflect evenness)¹ Most indices are easy to calculate and widely implemented in software packages (e.g., EstimateS and "vegan" in R)¹ 	 Many diversity indices exist, and it can be difficult to choose the most appropriate¹ Interpretation/communication not always straightforward¹ Insensitive to changes in community composition¹ (though this may be 	Nelder, 1989 ⁸ Zorn, 1998 ⁹ Royle & Nichols, 2003 ¹⁰ MacKenzie et al., 2006
Species diversity	β-diversity	 Can be used to track changes in community composition¹ Plays a critical role in effective conservation prioritization (e.g., designing reserve networks)¹ Important for detecting changes in the fundamental processes¹ 	 Many measures; no single best measure for all purposes¹ Comparing measures across space, time and studies can be very difficult¹ Scale-dependent (i.e., the size of the communities that are being included)¹ 	conditional on study design)	 11 Karanth & Nichols, 1998 12 Karanth, 1995 13 Clarke et al., 2023 14 Noss et al., 2003
Occupancy ³	Occupancy models ³	 Closed to changes in occupancy^[3] (abundance is constant)⁴ Sites and detections are independent⁴ The probability of occupancy and detection are constant across all sites 	 Does not require individual identification⁴ Just requires detection/non-detection data for each site¹ 	Occupancy ^[3] only measures distribution; it may be a misleading indicator of changes in abundance ¹ Interpretation/communication of results may not be straightforward (if the scale)	 Kelly et al., 2008 Moeller et al., 2018

Objective	<u>Approach</u>	<u>Assumptions</u>	Pros	Cons	References
		within a stratum or can be modelled using covariates ⁴ • Species are not misidentified ⁴	Relatively easy-to-use software exists for fitting models (PRESENCE, MARK, and the "unmarked" R package)¹ "Open" models exist that allow for the estimation of site colonization and extinction rates¹.⁴ Multi-species occupancy models[3] allow the inclusion of interactions among species while controlling for imperfect detection¹	of movement is much larger than the camera spacing the results should be interpreted as "probability of use" rather than occupancy) ¹	17 Chandler & Royle, 2013 18 Borchers & Efford, 2008 19 Efford, 2004 20 Royle & Young, 2008 21 Royle et al., 2009
Relative abundance indices	Poisson Zero-inflated Poisson (ZIP) ⁵ Negative binomial (NB) ⁶ Zero-inflated negative binomial (ZINB) ⁷ Hurdle models ⁸ Other	Since used for many approaches, many assumptions exist ¹	Simple to calculate and technically possible (even with small sample sizes when robust methods might fail)¹ Relative abundance indices often do correlate with abundance¹ Calibration with independent density estimates is possible¹	Difficult to draw inferences (a large number of <u>assumptions</u>); comparisons across space, time, species, and studies are difficult¹ Requires stringent <u>study design</u> (e.g., random sampling, standardized methods)¹	 22 O'Brien et al., 2011 23 Doran-Myers, 2018 24 Morin et al., 2022 25 Green et al., 2020 26 Parmenter et al., 2003 27 Noss et al.,
Absolute abundance; <u>Unmarked</u> <u>population</u>	Royle-Nichols model 9,10	Individual <u>detection probability</u> is constant ¹	Can relax <u>assumption</u> of constant abundance¹ Abundance is a fundamental parameter in wildlife research and monitoring¹ Can be applied to <u>unmarked</u> species¹ Only requires detection/non-detection data for each site (not counts)¹ May be used in models with <u>relative</u> <u>abundance</u> to control for <u>imperfect</u> <u>detection¹</u>	 Assumes a relatively specific relationship between local abundance and species-level detection probability¹ Depends on sampling area¹ Requires all or some of a population to be marked¹ No dedicated, simple software for this model (but can be implemented in MARK and the "unmarked" package in R)¹ 	²⁸ Sollmann et al., 2013a ²⁹ Sollmann et al., 2013b ³⁰ Rich et al., 2014 ³¹ Whittington et al., 2018 ³² Efford et al., 2009b
Population size / Absolute abundance / vital rates /	Capture- recapture (CR) / capture-mark- recapture (CMR) ^{11,12}	 Demographically closed (i.e., no births or deaths)¹ Geographically closed (i.e., no immigration or emigration)¹ 	May be used as a <u>relative abundance</u> <u>index</u> that controls for <u>imperfect</u> <u>detection</u> Easy-to-use software exists to implement (e.g., CAPTURE); MARK	Requires that individuals are distinguishable.¹ (However, CR ^[11,12] has also been used to estimate abundance of species that lack natural markers but that have phenotypic	³³ Royle et al., 2014

<u>Objective</u>	<u>Approach</u>	<u>Assumptions</u>	Pros	Cons	References
Density; Marked population		 Each individual has at least some probability of being captured² Overall sampled area should encompass full extent of individuals movements^{2,11} Activity centres are randomly dispersed and stationary¹³ 	Implements more complicated models with covariates (and must be used for mark-resight modelling)¹ • Can use the robust design with "open" models to obtain recruitment and survival rate estimates¹	and/or environment-induced characteristics ^{2,14,15} When the sample size is large enough to reliably estimate density with CR, ^[11,12] individuals are unlikely to have a unique marker ^{2,14,15}) • Dependent on the surveyed area, which is difficult to track and calculate ¹ • Requires a minimum number of captures and recaptures ¹ • Relatively stringent requirements for study design (e.g., no "holes" in the trapping grid) ¹ • Geographic closure at the plot level, which is often unrealistic ¹⁶ • Assumes a specific relationship between abundance and detection ¹ • Density cannot be explicitly estimated because the true area animals occupy is never measured (only approximated) ¹⁷	 34 Augustine et al., 2019 35 Burgar et al., 2018 36 Sun et al., 2022 37 Sollmann, 2018 38 Augustine et al., 2018 39 Davis et al., 2021 40 Rowcliffe et al., 2008 41 Rowcliffe et al., 2013 42 Rowcliffe et al., 2014 43 Rowcliffe et al., 2016
Density / population size; Marked population	Spatially explicit capture recapture (SECR) ¹⁸⁻²¹ (also referred to as Spatial capture-recapture [SCR])	 Individuals do not lose marks or are misidentified¹ All animals have an equal probability of capture (or, for spatially explicit models, an equal probability of capture for a given distance from the centre of their home range)¹ Captures of different individuals are independent¹ No behavioural response to being trapped or marked¹ Sampling occasions are independent¹ Population is demographically closed (i.e., no births or deaths)¹ For conventional models, geographically closed, i.e., no immigration or emigration)¹ 	 Produces direct estimates of density or population size for explicit spatial regions¹⁷ Allows researchers to mark a subset of the population/to take advantage of natural markings¹ Estimates are fully comparable across space, time, species and studies¹ Density estimates obtained in a single model, fully incorporate spatial information of locations and individuals¹ Both likelihood-based and Bayesian versions of the model have been implemented in relatively easy-to-use software (DENSITY and SPACECAP, respectively, as well as associated R packages)¹ 	 Requires that individuals are identifiable¹ Requires that a minimum number of individuals are trapped (each recaptured multiple times ideally)¹ Requires that each individual is captured at a number of camera locations¹ Multiple cameras per station may be required to identify individuals; difficult to implement at large spatial scales as it requires a high density of cameras¹³.²²⁴ May not be precise enough for long-term monitoring²⁵ Cameras must be close enough that individuals come into contact with multiple cameras¹.¹² 	 ⁴⁴ Rowcliffe et al., 2011 ⁴⁵ Cusack et al., 2015 ⁴⁶ Nakashima et al., 2017 ⁴⁷ Meek et al., 2016 ⁴⁸ Anile & Devillard, 2016 ⁴⁹ Huggard, 2018 ⁵⁰ Becker et al., 2022 ⁵¹ Warbington & Boyce, 2020

<u>Objective</u>	<u>Approach</u>	<u>Assumptions</u>	Pros	Cons	References
		Spatially explicit models have further assumption about animal movement. 1,18,21,22 These include: Home ranges do not change during the survey. Captures does not affect movement patterns. Random placement with respect to the distribution and orientation of home ranges. Distribution of home range centres follows a defined distribution (Poisson, or other, e.g.,).	• Flexibility in study design (e.g., "holes" in the trapping grid)¹ • "Open" SECR ^[18-21] models exist that allow for estimation of recruitment and survival rates¹ • "Avoid ad-hoc definitions of study area and edge effects"²³ • SECR ^[18-21] accounts for variation in individual detection probability; can produce spatial variation in density; SECR ^[18-21] more sensitive "to detect moderate-to-major populations changes" (+/-20-80%)¹³,24	½ MMDM (Mean Maximum Distance Moved) will usually lead to an under - estimation of home range size and thus overestimation of density 1.26.27	 52 Howe et al., 2017 53 Palencia et al., 2021 54 Gilbert et al., 2020 55 Twining et al., 2022 56 Bessone et al., 2020 57 Moeller et al., 2018
Marked population	Spatial mark-resight (SMR) (type of SCR model) 17,28,29	 Demographic and geographic closure of the population during the survey¹ Detections are independent²9 Detection probability decays with increasing distance of the camera from the activity centre²9,30 Animals have stable activity centres³0 Individual marks are not lost (for maximum precision), but SMR[17,28,29] does allow for inclusion of marked but unidentified resighting detections²8,31 The number of marked animals present is known before resightings²8,30 Animals are ungrouped²9 Counts of unmarked animals are modeled with a Poisson distribution³0 Cameras randomly placed with respect to activity centres²8 Marked animals are a random sample of the population with home ranges located inside the state space²9,30 All animals have stable activity centres within home ranges where detection probability is greatest²8,32 	 Estimates are fully comparable to SECR^[18-21] of marked species¹ Can be applied to a broader range of species than SECR^{[18-21]1} Allows researcher to take advantage of natural markings¹ Allows researcher to mark a subset of the population (note - precision is dependent on number of marked individuals in a population)¹ 	Animals may have to be physically captured and marked if natural marks do not exist on enough individuals¹ All individuals must be identifiable¹ Allows for density estimation for a unmarked population, but the precision of the density estimates are likely to be very low value¹ Remains poorly tested with camera data, although it offers promise¹ Density estimates are likely less precise than with SECR¹¹8-2¹¹ or REM, unless a large proportion of the population have marks¹ Requires sampling points to be close enough that individuals encounter multiple cameras¹	58 Loonam et al., 2021 59 Bridges & Noss, 2011 60 Rovero & Zimmermann, 2016 61 Borchers & Marques, 2017

Objective	<u>Approach</u>	Assumptions	Pros	Cons	References
Density; Unmarked population	Spatial count (SC) (type of SCR model) ^{17,33}	 Camera must be close enough together that animals are detected at multiple cameras^{13,17} Population closure^{13,17} 	Does not require individual identification ¹³	Produces imprecise estimates even under ideal circumstances unless it is supplemented with auxiliary data (e.g., telemetry) ^{17,23,28,29}	
		 Independence of detections^{13,17} Activity centres randomly dispersed^{13,17} Activity centres are stationary^{13,17} 		Precision decreases with an increasing number of individuals detected at a camera" ²⁴ (as overlap of home ranges of individuals' increases) ^{13,34}	
				Not appropriate for low <u>density</u> or elusive species when recaptures too few to confidently infer the number and location of activity centres" ^{13,35}	
				Not appropriate for high-density populations with evenly spaced activity centres (camera[-specific] counts will be too similar and impair activity centre inference)"	
				Ill-suited to populations that exhibit group-travelling behaviour" ^{13,36}	
				Study design (camera arrangement) can dramatically affect the accuracy and precision of density estimates" ^{13,37}	
				Cameras must be close enough that animals are detected at multiple <u>camera locations</u> (may be challenging to implement at large scales as many cameras are needed)**13,17*	
Density / population size; Partially Marked	Spatial Partial Identity Model (Categorical SPIM; catSPIM) ^{13,34,36}	Same as <u>SC</u> ^{13,34,36} Each categorical identifier (e.g., <u>Sex</u> <u>Class</u> , collar, etc) has fixed number of possibilities (e.g., male/female, collared/not collared) ³⁶	May produce more precise and less biased <u>density</u> estimates than <u>SC</u> with less information ^{13,36}	Sensitive to non-independent movement (e.g., group-travel; can cause over-dispersion and bias estimates ^{13,36}); may limit application to solitary species only ^{13,36}	
population	(Extension of <u>SC</u> model using animal traits (e.g.	All possible values of categorical identifiers occur in the population with probabilities that can be estimated ^{13,34,36}		May produce be less reliable/accurate estimates for high-density populations ^{13,36}	
	Sex Class, antler points) and model parameters)	Every individual is assigned "full categorical identity" (i.e., "set of traits given all categorical identifiers and possibilities") ^{13,34}		To few categorical identifiers/ possibilities can result in mis- assignments and overestimating density 13,34,26	

<u>Objective</u>	<u>Approach</u>	Assumptions	Pros	Cons	References
		There is no change in an individual's identity trait during the <u>survey</u> period (e.g., antlers present/absent) ³⁴			
Density / population size; Partially Marked population	Spatial Partial Identity Model (2- flank SPIM) ^{13,38} (extension of SCR model augmented with data from partially- identifying images)	 Same as <u>SCR</u>^{13,38} Capture processes for left-side, right-side and both-side images are independent ^{13,38} 	 Same as <u>SCR</u>^{13,38} Improved precision of <u>density</u> estimates relative to <u>SCR</u>^{13,38,39} Many study designs can be used (<u>paired sample stations</u>, single <u>camera locations</u>, and hybrids of both <u>paired</u>-and single <u>camera locations</u>^{13,38,39} Can be used with single-camera and hybrid sampling designs, and therefore requires fewer cameras (or sample more area) than <u>SCR</u>^{13,38} May be more robust to non-independence than <u>SC</u>^{34,38} 	 Computationally intensive^{13,38} Increased precision is less pronounced in high-density populations^{13,38} 	
Density; Unmarked	Random encounter models (REM) ^{40,41}	 Demographic and geographic closure^{23,40} Random with respect to animal movement^{1,40} Animal movement is not affected by the cameras^{1,40} Independent "contacts" between camera locations can be accurately counted^{1,40} Unbiased estimates of animal activity levels and animal speed can be obtained^{1,42,43} Camera's detection zone can be approximated well using a 2D cone shape, defined by the radius and angle parameters⁴⁴ If activity and speed are to be estimated from camera data, two additional assumption: All animals are active during the peak daily activity⁴² Animals moving quickly past a camera are not missed⁴³ 	 Flexible study design (e.g., "holes" in grids allowed, camera spacing less important)¹ Can be applied to unmarked species¹ Allows community-wide density estimation¹ Outputs also include informative parameter estimates (i.e., animal speed and activity levels, and detection zone parameters)¹ Comparable estimates to SECR^{[18-21]1} Does not require marked animals or identification of individuals^{23,40} Can use camera spacing without regard to population home range size^{23,40} Direct estimation of density; avoids adhoc definitions of study area⁴⁰ 	 Requires relatively stringent study design, particularly (e.g., random sampling and use of bait or lure)¹ Requires independent estimates of animal speed or measurement of animal speed within videos¹ No dedicated, simple software¹ Random relative to animal movement, grid preferred, avoid multiple captures of same individual, area coverage important for abundance estimation² Possible sources of error include inaccurate measurement of detection zone and movement rate⁴¹,⁴⁵ 	

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<u>Objective</u>	Approach	<u>Assumptions</u>	Pros	Cons	References
Density; Unmarked	Random encounter and staying time (REST) ⁴⁶	 The population is closed (animal density is constant during the survey)⁴⁰ The detection probability is perfect¹ (p = 1) unless otherwise modelled⁴⁶ Camera locations are representative of the available habitat⁴⁶ Cameras are randomly placement with respect to the spatial distribution of animals⁴⁶ Animal movement and behaviour are not affected by cameras⁴⁶ Observations are independent⁴⁶ The observed distribution of staying time in the focal area fits the distribution of movement⁴⁶ The observed staying time must follow a given parametric distribution⁴⁶ 	Provides unbiased estimates of animal density, even when animal movement speed varies, and animals travel in pairs ⁴⁶	 Attraction or aversion to cameras is exhibited in some species⁴⁷ and could affect the time within the <u>detection zone</u> and subsequently affect estimates of <u>density</u>²³ Requires accurate measurements of the area of the camera <u>detection zone</u>, which has been a challenge in previous studies^{23,44-46,48} Mathematically challenging⁴⁵ 	
Density; Unmarked	Time in front of the camera (TIFC) ⁴⁹⁻⁵¹	 Cameras are placed randomly, or representative relative to animal movement⁵⁰ No influence of cameras on animal movement⁵⁰ Reliable detection of animals in part of the camera's FOV (at least)⁵⁰ 	 Does not require individual identification⁵¹ Makes no <u>assumption</u> about home range⁵¹ Comparable to estimates from <u>SECR</u>^{[18-21]51} 	 Requires careful calculation of the effective area of detection⁵¹ A high level of measurement error⁵⁰ 	
Density; Unmarked	Distance sampling (DS) ^{52,61}	 Random or systematic random placements consistent with the assumption that points are placed independently of animal locations⁵² Placed randomly with respect to animal movement ⁵³ Certain detection at distance 0⁵³ Certain detection at focal area⁵³ Closed population⁵³ Animal movement and behaviour not affected by the cameras⁵³ 	 A shortcut to controlling for variation in detection distances by only counting individuals within a short distance with an unobstructed view, and well sampled across cameras and species¹ Density estimates are unbiased by animal movement "since camera-animal distance is measured at a certain instant in time (intervals of duration t apart)"^{13,52} Can be applied to low-density populations^{13,53} 	May require discarding a portion of the dataset (when the best fitting model truncates the dataset) ¹ Biased by movement speed ⁵³ Best suited to larger animals; the smaller the focal species, the lower [wildlife] cameras must be set, which reduces the depth of the viewshed, and thus sampling size and the flexibility of the model" 13,52 Does not permit inference about spatial variation in abundance (unless using hierarchical distance which can model	

<u>Objective</u>	Approach	<u>Assumptions</u>	Pros	Cons	References
		 Animals detected at initial locations (e.g., they do not change course in response to the camera prior to detection)⁵³ Distances are measured exactly (however if the data from different distances will be grouped ("binned") for analysis later, an accuracy of +/- 1m may suffice)⁵³ Observations are independent events⁵³ Snapshot moments selected independently of animal locations⁵³ 	Does not require individual identification ⁵²	spatial variation as a function of covariates) ^{13,54} • "Calculating camera-animal distances can be labour-intensive and time-consuming (However, recently developed techniques (e.g., Johanns et al., 2022) show promise for simplifying and automating the process) ¹³ • Requires good understanding of the focal populations' activity patterns; density estimates can be biased (e.g., under-estimated) when regular periods of inactivity are not accounted for (using detection times to infer periods of activity may help overcome this limitation)**13,52,53* • Tends to underestimate density** • Low population density and reactivity to cameras may be major sources of bias**13,56*	
Density; Unmarked	Time-to-event (TTE) model ⁵⁷	 Demographic and geographic closure^{57,58} Locations <u>randomly placed</u>, <u>systematic</u>, <u>systematic random⁵⁷</u> <u>Independent detections</u> in space and time⁵⁷ Spatial counts of animals (or counts in equal subsets of the landscape) are <u>Poisson</u>-distributed⁵⁸ Accurate estimate of movement speed⁵⁸ 	Can be efficient for estimating abundance of common species (with a lot of images) ⁵⁷	 Requires independent estimates of movement rate (difficult to attain without telemetry data)⁵⁷ Assumes that <u>detection probability</u> is 1 (or apply extension to account for <u>imperfect detection</u>)⁵⁷ 	
Density; Unmarked	Space-to-event (STE) models ⁵⁷	 Demographic and geographic closure⁵⁷ Locations randomly placed^V Independent detections in space and time⁵⁷ Spatial counts of animals in a small area (or counts in equal subsets of the landscape) are Poisson-distributed⁵⁸ 	 Can be efficient for estimating abundance of common species (with a lot of images)⁵⁷ Does not require estimate of movement rate⁵⁷ 	Assumes that <u>detection probability</u> is 1 ⁵⁷	

Objective	Approach	Assumptions	Pros	Cons	References
Density; Unmarked	Instantaneous sampling (IS) ⁵⁷	 Demographic and geographic closure⁵⁷ Locations randomly placed⁵⁷ <u>Independent detections</u> in space and time⁵⁷ 	 Can be efficient for estimating abundance of common species (with a lot of images)⁵⁷ Flexible <u>assumption</u> of animals' distribution⁵⁷ 	 Requires accurate counts of animals⁵⁷ Assumes that <u>detection probability</u> is 1⁵⁷ Reduced precision⁶⁷ 	
Behaviour (Diel activity poldness, etc	patterns, mating,	Assumptions vary depending on the behavioural metric¹ For studies of activity patterns and temporal interactions of species: activity level is the only factor determining detection rates; animals are active when camera detection rate reaches its maximum in daily cycle³3,60	 Can detect difficult to observe behaviours (i.e., boldness, or mating)⁵⁹ Long-term data on behavioural changes that would be difficult to obtain otherwise (i.e., time-limited human observers, or costly GPS collars)⁵⁹ Can monitor behaviour in response to specific locations (i.e., compost sites, which might be more difficult using GPS collars for example)⁶⁰ Can evaluate interactions between species⁶⁰ 	 Behavioural metrics may not reflect the behavioural state (inferred)⁶⁰ Biases associated with equipment (i.e., presence of the camera itself may change behaviour studied)⁶⁰ Difficult to consider individual variation⁶⁰ 	