11.0 Appendix A

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

Objective	Approach	Assumptions	Pros	Cons	References
Species inventory	Species inventory	• No formal assumptions[1]	• Maximum flexibility for study design (e.g., camera days per camera location or use of lure[2])[1]	• Not reliable estimates for inference ("considered as unfinished, working drafts")[1]	[1] Wearn & Glover-Kapfer, 2017 [2] Rovero et al., 2013 [3] MacKenzie et al., 2002 [4] MacKenzie et al., 2006 [5] Rowcliffe & Carbone, 2008 [6] Lambert, 1992 [7] Mullahy, 1986 [8] McCullagh & Nelder, 1989 [9] Heilbron 1994 [10] Karanth & Nichols, 1998 [11] Karanth, 1995 [12] Clarke et al., 2023
Species richness	Species richness	• Camera locations are randomly placed[1] • Camera locations are independent[1] • Detection probability of different species remains the same[1] ("true" species richness estimation involves attempting to correct for "imperfect detection"[1]) • Sampling effort is comparable between camera locations[31]	• Fundamental to ecological theory and often a key metric used in management[1] • Simple to analyze, interpret and communicate[1] • 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 disregarded[1] • Insensitive to changes in abundance, community structure and community composition[1]	
Species diversity	Species diversity	• Camera locations are randomly placed[1] • Camera locations are independent[1] • Detection probability of different species remains the same[1]	• 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 indices exist, and it can be difficult to choose the most appropriate[1] • Comparing measures across space, time and studies can be very difficult[1] • Insensitive to changes in community composition[1] (however, this may be conditional on study design)	
Species diversity	β-diversity	• Camera locations are randomly placed[1]	• Can be used to track changes in community composition[1]	• No single best measure for all purposes[1]	

Objective	Approach	Assumptions	Pros	Cons	References
		• Randomness and independence[1] • Samples are assumed to have been taken at random from the broader population of sites[1]	• Plays a critical role in effective conservation prioritization (e.g., designing reserve networks)[1] • Important for detecting changes in the fundamental processes[1]	• Interpretation/communication not always straightforward[1] • Scale-dependent (i.e., influenced by the size of the communities that are being included)[1]	[13] Noss et al., 2003 [14] Kelly et al., 2008 [15] Moeller et al., 2018 [16] Chandler & Royle, 2013 [17] Royle et al., 2009 [18] Borchers & Efford, 2008 [19] Efford, 2004 [20] Royle & Young, 2008 [21] O'Brien et al., 2011 [22] Doran-Myers, 2018 [23] Morin et al., 2022 [24] Green et al., 2020 [25] Parmenter et al., 2003 [26] Noss et al., 2012 [27] Sollmann et al., 2013a
Occupancy[3]	Occupancy models[3]	• Occupancy is constant[3] (abundance is constant)[4] • Camera locations are independent[4] • Detections are independent[4] • The probability of occupancy and detection are constant across all camera locations within a stratum or can be modelled using covariates[4] • Species are not misidentified[4]	• Does not require individual identification[4] • Only requires detection/non-detection data for each site[1] • 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 rates[1,4] • Multi-species occupancy models[3] allow the inclusion of interactions among species while controlling for imperfect detection[1]	• 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 of movement is much larger than the camera spacing the results should be interpreted as "probability of use" rather than occupancy)[1]	
Relative abundance indices	Poisson Zero-inflated Poisson (ZIP)[6] Negative binomial (NB)[7]	• Many assumptions exist (since used for many approaches)[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 abundance[1]	• Difficult to draw inferences (a large number of assumptions); comparisons across space, time, species, and studies are difficult[1] • Requires stringent study design (e.g., random sampling, standardized methods)[1]	

Objective	Approach	Assumptions	Pros	Cons	References
	Zero-inflated negative binomial (ZINB)[8]		• Calibration with independent density estimates is possible[1]	• Detection rates from remote cameras cannot be used as an index to compare relative abundance across species[5]	[28] Sollmann et al., 2013b [29] Rich et al., 2014 [30] Whittington et al., 2018 [31] Royle & Nichols, 2003
	Hurdle models[7,9]				
	Other				
Population size / Absolute abundance / vital rates / Density; Marked population	Capture-recapture (CR) / capture-mark-recapture (CMR)[10,11]	• Demographic closure (i.e., no births or deaths)[1] • Geographic closure (i.e., no immigration or emigration)[1] • All individuals have at least some probability of being detected[2] • Sampled area encompasses the full extent of individuals' movements[2,10] • Activity centres are randomly dispersed[12] • Activity centres are stationary[12]	• May be used as a relative abundance index that controls for imperfect detection[1] • Easy-to-use software exists to implement (e.g., CAPTURE); MARK 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 estimates[1]	• Requires that individuals are distinguishable.[1] However, CR[10,11] has also been used to estimate abundance of species that lack natural markers but that have phenotypic and/or environment-induced characteristics[2,13,14] • When the sample size is large enough to reliably estimate density with CR, [10,11] individuals are unlikely to have a unique marker[2,13,14] • 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[1]	[32] Efford et al., 2009b [33] Royle et al., 2014 [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

Objective	Approach	Assumptions	Pros	Cons	References
				• 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)[16]	[42] Rowcliffe et al., 2014 [43] Rowcliffe et al., 2016 [44] Rowcliffe et al., 2011 [45] Cusack et al., 2015 [46] Nakashima et al., 2018 [47] Meek et al., 2016 [48] Anile & Devillard, 2016 [49] Huggard, 2018 [50] Becker et al., 2022 [51] Warbington & Boyce, 2020 [52] Howe et al., 2017 [53] Borchers & Marques, 2017 [54] Palencia et al., 2021 [55] Gilbert et al., 2021

Density / population size; Marked population	Spatially explicit capture recapture (SECR)[17–20] (also referred to as Spatial capture-recapture [SCR])	• Demographic closure (i.e., no births or deaths)[1]
		• Detection probability of different individuals is equal[1]
		  ○ or, for SECR, individuals have equal detection probability at a given distance from the centre of their home range[1]
		• Detections of different individuals are independent[1]
		• Behaviour is unaffected by cameras and marking[1]
		• Individuals do not lose marks[1]
		• Individuals are not misidentified[1]
		• Surveys are independent[1]
		• For conventional models, geographic closure (i.e., no immigration or emigration)[1]
		• Spatially explicit models have further assumptions about animal movement[1,17,21]; these include:
		  ○ Home ranges are stable[1]
		  ○ Movement is unaffected by cameras[1]
		  ○ Camera locations are randomly placed with respect to the
			• Produces direct estimates of density or population size for explicit spatial regions[16]
			• Allows researchers to mark a subset of the population/to take advantage of natural markings[1]
			• Estimates are fully comparable across space, time, species and studies[1]
			• Density estimates obtained in a single model, fully incorporate spatial information of locations and individuals[1]
			• 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]
			• Flexibility in study design (e.g., "holes" in the trapping grid)[1]
			• "Open" SECR[17–20] models exist that allow for estimation of recruitment and survival rates[1]
			• "Avoid ad-hoc definitions of study area and edge effects"[22]
				• Requires that individuals are identifiable[1]
				• 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 locations[1]
				• Multiple cameras per station may be required to identify individuals; difficult to implement at large spatial scales as it requires a high density of cameras[12,23]
				• May not be precise enough for long-term monitoring[24]
				• Cameras must be close enough that animals are detected at multiple camera locations[1] (may be challenging to implement at large scales as many cameras are needed)"[16]
				• ½ MMDM (Mean Maximum Distance Moved) will usually lead to an under -estimation of home range size and thus overestimation of density[1,25,26]	

Objective	Approach	Assumptions	Pros	Cons	References
		distribution and orientation of home ranges[1] ○ Distribution of home range centres follows a defined distribution (Poisson, or other, e.g., negative binomial)[1]	• SECR[17–20] accounts for variation in individual detection probability; can produce spatial variation in density; SECR[17–20] more sensitive "to detect moderate-to-major populations changes" (+/-20-80%)[12,23]		[56] Twining et al., 2022 [57] Bessone et al., 2020 [58] Loonam et al., 2021 [59] Bridges & Noss, 2011 [60] Rovero & Zimmermann, 2016
Density; Marked population	Spatial mark-resight (SMR) (type of SCR model)[16,27,28]	• Demographic closure (i.e., no births or deaths)[12,16] • Geographic closure (i.e., no immigration or emigration)[12,16] • Individuals do not lose marks[1] (for maximum precision), but SMR[16,27,28] does allow for inclusion of marked but unidentified resighting detections[27,29] • Individuals are not misidentified[1] • Failure to identify marked individuals is random[12,30] • Marked animals are a random sample of the population with home ranges located inside the state space[28,29] • Detections are independent[12,16] • Individuals have equal detection probability at a given distance from the centre of their home range[1] • Detections of different individuals are independent[1] • Movement is unaffected by cameras[1] • Behaviour is unaffected by cameras and marking[1] • Camera locations are randomly placed relative to the distribution and orientation of home ranges[1]	• Estimates are fully comparable to SECR[17–20] of marked species[1] • Can be applied to a broader range of species than SECR[17–20]1 • Allows researcher to take advantage of natural markings[1] • 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 individuals[1] • All individuals must be identifiable[1] • Allows for density estimation for a unmarked population, but the precision of the density estimates are likely to be very low value[1] • Remains poorly tested with camera data, although it offers promise[1] • Density estimates are likely less precise than with SECR[17–20] or REM, unless a large proportion of the population have marks[1] • Requires sampling points to be close enough that individuals encounter multiple cameras[1]	

Objective	Approach	Assumptions	Pros	Cons	References
		• Camera locations are close enough together that animals are detected at multiple cameras[12,16] • Surveys are independent[1] • Home ranges are stable[1] • Distribution of home range centres follows a defined distribution (Poisson, or other, e.g., negative binomial)[1] • Animals' activity centres are randomly dispersed[12,16] • Animals' activity centres are stationary[12,16] • All animals have stable activity centres within home ranges where detection probability is greatest[27,31,32]			
Density; Unmarked population	Spatial count (SC) / Unmarked spatial capture-recapture (type of SCR model)[16,33]	• Camera locations are close enough together that animals are detected at multiple cameras[12,16] • Demographic closure (i.e., no births or deaths)[12,16] • Geographic closure (i.e., no immigration or emigration)[12,16] • Detections are independent[12,16] • Animals' activity centres are randomly dispersed[12,16] • Animals' activity centres are stationary[12,16]	• Does not require individual identification[12]	• Produces imprecise estimates even under ideal circumstances unless supplemented with auxiliary data (e.g., telemetry)[16,22,27,28] • Precision decreases with an increasing number of individuals detected at a camera"[23] (as overlap of individuals' home ranges increases) [12,34] • Not appropriate for low density or elusive species when recaptures too few to confidently infer the number and location of activity centres"[12,35] • Not appropriate for high-density populations with evenly spaced activity centres (camera[-specific] counts will be too similar and impair activity centre inference)"[12]	

Objective	Approach	Assumptions	Pros	Cons	References
				• Ill-suited to populations that exhibit group-travelling behaviour"[12,36] • Study design (camera arrangement) can dramatically affect the accuracy and precision of density estimates"[12,37] • Cameras must be close enough that animals are detected at multiple camera locations (may be challenging at large scales as many cameras are needed)"[12,16]	
Density / population size; Partially Marked population	Spatial Partial Identity Model (Categorical SPIM; catSPIM)[34,36] (Extension of SC model using animal traits (e.g., Sex Class, antler points) and model parameters)	• Same as SC[12,34,36] ○ Camera must be close enough together that animals are detected at multiple cameras[12,16] ○ Demographic closure (i.e., no births or deaths)[12,16] ○ Geographic closure (i.e., no immigration or emigration)[12,16] ○ Detections are independent[12,16] • Activity centres are randomly dispersed[12,16] • Activity centres are stationary[12,16] • Each categorical identifier (e.g., male/female, collared/not collared, etc) has fixed number of possibilities[36] • All possible values of categorical identifiers occur in the population with probabilities that can be estimated[12,34,36] • Every individual is assigned "full categorical identity" (i.e., "set of	• May produce more precise and less biased density estimates than SC with less information[12,36]	• Sensitive to non-independent movement (e.g., group-travel; can cause over-dispersion and bias estimates[12,36]); may limit application to solitary species only[12,36] • May produce be less reliable/accurate estimates for high-density populations[12,36] • Too few categorical identifiers/ possibilities can result in mis-assignments and overestimating density[12,25,34]	

Objective	Approach	Assumptions	Pros	Cons	References
		traits given all categorical identifiers and possibilities")[12,34] • Individuals' identifying traits do not change during the survey (e.g., antlers present/absent)[34]			
Density / population size; Partially Marked population	Spatial Partial Identity Model (2-flank SPIM)[38] (extension of SCR model augmented with data from partially-identifying images)	• Same as SCR[12,38] • Capture processes for left-side, right-side and both-side images are independent[12,38]	• Same as SCR[12,38] • Improved precision of density estimates relative to SCR[12,38,39] • Many study designs can be used (paired sample stations, single camera locations, and hybrids of both paired- and single camera locations[12,38,39] • Can be used with single-camera and hybrid sampling designs, and therefore requires fewer cameras (or sample more area) than SCR[12,38] • May be more robust to non-independence than SC[12,38]	• Computationally intensive[12,38] • Increased precision is less pronounced in high-density populations[12,38]	
Density; Unmarked	Random encounter models (REM)[40,41]	• Demographic closure[22,40] (i.e., no births or deaths) • Geographic closure[22,40] (i.e., no immigration or emigration) • Camera locations are randomly placed relative to animal movement[1,40] • Animal movement is unaffected by the cameras[1,40] • Accurate counts of independent "contacts" camera locations[1,40] • Unbiased estimates of animal activity levels and speed[1,42,43] • Camera's detection zone can be approximated well using a 2D cone	• Flexible study design (e.g., "holes" in grids allowed, camera spacing less important)[1] • Can be applied to unmarked species[1] • Allows community-wide density estimation[1] • Outputs also include informative parameter estimates (i.e., animal speed and activity levels, and detection zone parameters)[1] • Comparable estimates to SECR[[17–20]][1]	• 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 videos[1] • No dedicated, simple software[1] • Random relative to animal movement, grid preferred, avoid multiple captures of same individual, area coverage important for abundance estimation[2] • Possible sources of error include inaccurate measurement of	

Objective	Approach	Assumptions	Pros	Cons	References
		shape, defined by the radius and angle parameters[44] • If activity and speed are to be estimated from camera data, two additional assumptions: • All animals are active during the peak daily activity[42] • Animals moving quickly past a camera are not missed[43]	• Does not require marked animals or identification of individuals[22,40] • Can use camera spacing without regard to population home range size[22,40] • Direct estimation of density; avoids ad-hoc definitions of study area[40]	detection zone and movement rate[41,45]	
Density; Unmarked	Random encounter and staying time (REST)[46]	• Demographic closure (i.e., no births or deaths) and geographic closure (i.e., no immigration or emigration) (animal density is constant during the survey)[40] • Detection is perfect[1] (detection probability “p” = 1) unless otherwise modelled[46] • Camera locations are representative of the available habitat[46] • Camera locations are randomly placed relative to the spatial distribution of animals[46] • Animal movement and behaviour are not affected by cameras[46] • Detections are independent[46] • The observed distribution of staying time in the focal area fits the distribution of movement[46] • The observed staying time must follow a given parametric distribution[46]	• 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 species[47] and could affect the time within the detection zone and subsequently affect estimates of density[22] • Requires accurate measurements of the area of the camera detection zone, which has been a challenge in previous studies[22,44–46,48] • Mathematically challenging[45]	
Density; Unmarked	Time in front of the camera (TIFC)[49–51]	• Camera locations are randomly placed or representative relative to animal movement[50] • Movement is unaffected by the cameras[50]	• Does not require individual identification[51] • Makes no assumption about home range[51]	• Requires careful calculation of the effective area of detection[51] • A high level of measurement error[50]	

Objective	Approach	Assumptions	Pros	Cons	References
		• Reliable detection of animals in part of the camera's FOV (at least)[50]	• Comparable to estimates from SECR[17–20][51]		
Density; Unmarked	Distance sampling (DS)[52,53]	• Random or systematic random placements (consistent with the assumption that points are placed independently of animal locations)[52] • Camera locations are randomly placed relative to animal movement[54] • Detection is perfect (detection probability "p" = 1) at focal area / distance 0[54] • Demographic closure (i.e., no births or deaths) and geographic closure (i.e., no immigration or emigration) (animal density is constant during the survey)[54] • Animal movement and behaviour are unaffected by the cameras[54] • Animals are detected at initial locations (e.g., they do not change course in response to the camera prior to detection)[54] • Distances are measured exactly (however if the data from different distances will be grouped ("binned") for analysis later, an accuracy of +/- 1m may suffice)[54] • Detections are independent[54] • Snapshot moments selected independently of animal locations[54]	• 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 species[1] • Density estimates are unbiased by animal movement "since camera-animal distance is measured at a certain instant in time (intervals of duration *t* apart)"[12,52] • Can be applied to low-density populations[12,52] • Does not require individual identification[52]	• May require discarding a portion of the dataset (when the best fitting model truncates the dataset)[1] • Biased by movement speed[54] • Best suited to larger animals; the smaller the focal species, the lower remote cameras must be set, which reduces the depth of the viewshed, and thus sampling size and the flexibility of the model"[12,52] • Does not permit inference about spatial variation in abundance (unless using hierarchical distance which can model spatial variation as a function of covariates)[12,55] • "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)"[12] • Requires a 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)"[12,52,54] • Tends to underestimate density[12,52,56]	

Objective	Approach	Assumptions	Pros	Cons	References
				• Low population density and reactivity to cameras may be major sources of bias"[12,57]	
Density; Unmarked	Time-to-event (TTE) model[15]	• Demographic closure (i.e., no births or deaths)[15,58] • Geographic closure (i.e., no immigration or emigration) at the level of the sampling frame (area of interest); this assumption does not apply at the plot-level (area sampled by the camera)[15,58] • Animal movement and behaviour are unaffected by the cameras[54] • Camera locations placement is random, systematic, or systematic random[15] • Detections are independent[15] • Spatial counts of animals (or counts in equal subsets of the landscape) are Poisson-distributed[58] • Accurate estimate of movement speed[58] • Detection is perfect (detection probability "*p*" = 1)[15]	• Can be efficient for estimating abundance of common species (with a lot of images)[15]	• Requires independent estimates of movement rate (difficult to obtain without telemetry data)[15] • Assumes that detection probability is 1 (or apply extension to account for imperfect detection)[15]	
Density; Unmarked	Space-to-event (STE) models[15]	• Demographic closure (i.e., no births or deaths)[15] • Geographic closure (i.e., no immigration or emigration)[15] • Camera locations are randomly placed[15] • Detections are independent[15] • Spatial counts of animals in a small area (or counts in equal subsets of the landscape) are Poisson-distributed[58]	• Can be efficient for estimating abundance of common species (with a lot of images)[15] • Does not require estimate of movement rate[15]	• Assumes that detection probability is 1[15]	

Objective	Approach	Assumptions	Pros	Cons	References
		• Detection is perfect (detection probability "*p*" = 1)[15]			
Density; Unmarked	Instantaneous sampling (IS)[15]	• Demographic closure (i.e., no births or deaths)[15] • Geographic closure (i.e., no immigration or emigration)[15] • Camera locations are randomly placed[15] • Detections are independent[15] • Detection is perfect (detection probability "*p*" = 1)[15]	• Can be efficient for estimating abundance of common species (with a lot of images)[15] • Flexible assumption of animals' distribution[15]	• Requires accurate counts of animals[15] • Assumes that perfect (detection probability "*p*" = 1)[15] • Reduced precision[15]	
Behaviour (diel activity patterns, mating, boldness, etc.)		• Assumptions vary depending on the behavioural metric[1] • 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 cycle[33,60]	• 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 species[60]	• 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 variation[60]	