Methods in Ecology and Evolution

Fast, flexible alternatives to regular grid designs for spatial capture-recapture

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Abstract

1. Spatial capture-recapture (SCR) methods use the location of detectors (camera traps, hair snares, live-capture traps) and the locations at which animals were detected (their spatial capture histories) to estimate animal density. Despite the often large expense and effort involved in placing detectors in a landscape, there has been relatively little work on how detectors should be located. A natural criterion is to place traps so as to maximize the precision of density estimators, but the lack of a closed-form expression for precision has made optimizing this criterion computationally demanding.
2. Recent results by Efford and Boulanger (2019) show that precision can be well approximated by a function of the expected number of detected individuals and expected number of recapture events, both of which can be evaluated at low computational cost. We use these results to develop a method for obtaining survey designs that optimize this approximate precision for SCR studies using count or binary proximity detectors, or multi-catch traps.
3. We show how the basic design protocol can be extended to incorporate spatially-varying distributions of activity centres and animal detectability. We illustrate our approach by simulating from a camera trap study of snow leopards in Mongolia and comparing estimates from our designs to those generated by regular or optimized grid designs. Optimizing detector placement increased the number of detected individuals and recaptures, but this did not always lead to more precise density estimators due of less precise estimation of the effective sampling area. In most cases the precision of density estimators was comparable to that obtained with grid designs, with improvement in some scenarios where approximate $CV(\hat{D}) < 20\%$ and density varied spatially.
4. Designs generated using our approach are transparent and statistically grounded. They can be produced for survey regions of any shape, adapt to known information about animal density and detectability, and are potentially easier and less costly to implement. We recommend their use as good, flexible candidate designs for SCR surveys when reasonable knowledge of model parameters exists. We provide software for researchers to construct their own designs, in the form of updates to design functions in the R package *oSCR*.

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1 Introduction

Spatial capture-recapture (SCR) models are commonly used to estimate animal abundance and distribution from surveys that use detectors at fixed locations to record the presence of marked animals at those locations, in the form of spatial capture histories (Borchers & Efford, 2008; Royle, Chandler, Sollmann, & Gardner, 2014). Detection data can be collected by camera traps, hair snares and scat surveys, live-capture traps, area searches, or acoustic detectors, with presence recorded accordingly as an image, DNA sample, animal, or audio recording. SCR methods jointly estimate the parameters of a spatial model quantifying expected animal activity centre density at all points in the survey region, and a detection model that quantifies the probabilities of detection, given the activity centre locations and the detector locations.

All SCR surveys have to decide where to place detectors to best address survey objectives. For wildlife surveys, the focus is often animal density or abundance, and survey designs ideally minimize the mean square error of density (or abundance) estimators, equal to the square of the bias plus the variance. SCR estimators have been shown to be unbiased under a wide range of detector arrangements (Efford, 2019a; Efford & Boulanger, 2019; Sun, Fuller, & Royle, 2014), so that designs that maximize the precision of density (or abundance) estimators – or equivalently, minimize the coefficient of variation of the density estimator $CV(\hat{D})$ – could reasonably be considered optimal (Efford & Boulanger, 2019; Royle et al., 2014).

The SCR survey design goal we consider here is to choose the locations of a fixed number of detectors in a survey region so as to minimize $CV(\hat{D})$, without any further constraints on detector locations (for example, that these must lie on a regular grid). There is currently no method for doing this, which is surprising given the monetary cost and effort involved in setting up an SCR survey. The reason is that until recently the only way to calculate variance (as well as bias) with a given design was by computationally demanding simulation, requiring that an SCR model be fit to each of a large enough number of simulated datasets to achieve stable estimates. This allows small numbers of candidate designs to be compared (Clark, 2019; Efford, 2019b; Kristensen & Kovach, 2018; Sollmann, Gardner, & Belant, 2012; Sun et al., 2014), but optimizing detector locations requires potentially thousands of evaluations, and this has been computationally prohibitive. As a result, decisions about how to modify candidate designs and when to stop the design process have been left to subjective judgement. Exceptions are Royle et al. (2014) and Dupont, Royle, Nawaz, and Sutherland (2020), who considered designs optimizing a suite of objective functions, which are either related only indirectly to the main objective of estimating animal density precisely by focusing on detection parameters, or relied on simplifying assumptions that are untested and available only for certain types of detection models.

As a result, most SCR surveys use some combination of broad guidelines on detector spacing and layout to generate a small set of candidate designs, possibly followed by a simulation-based comparison of these candidate designs on statistical criteria such as relative bias and precision. Being general, guidelines typically recommend highly regular designs that arrange detectors in a regularly-spaced grid, or else in clusters, with the spacing between detectors chosen so that individual animals have a reasonable chance of being detected at more than one detector (Clark, 2019; Efford & Fewster, 2013). The motivation for using these designs is that they can be expected to return unbiased density estimates with relatively good precision under a wide range of conditions (Efford & Fewster, 2013). However, placing detectors at regular intervals may be impossible in some survey areas, and better designs may be achievable without the constraint of regular spacing even if that spacing is feasible (Dupont et al., 2020).

The only way to compute bias in SCR-based density estimates remains by computationally intensive simulation, but a recent approximation of $CV(\hat{D})$ (Efford & Boulanger, 2019) provides a sensible, computationally feasible design criterion for optimizing detector locations with unbiased estimators. Their approximation is

$$CV(\hat{D}) \approx 1/\sqrt{\min\{E(n), E(r)\}} \quad (1)$$

where both the expected number of first captures $E(n)$ and recaptures $E(r)$ can be evaluated quickly using numerical integration over a habitat mask of the survey region. Two main uses for the approximation are suggested: fast comparison of candidate designs, and optimizing detector spacing for a regular grid of detectors by numerically finding the spacing for which $E(n) = E(r)$. In this paper we show how this approximation can be combined with optimization methods to determine detector locations that maximize the approximate precision of density estimates, without constraint to a regular layout. The resulting detector locations reflect the best available balance between a wide spacing that results in few recaptures but detects many individuals, and clustering detectors close together so that an animal seen on one detector will likely be seen at others (Royle et al., 2014; Sollmann et al., 2012). We call these $\min(n, r)$ designs.

Calculations of $E(n)$ and $E(r)$ remain fast even if their inputs vary spatially, for example as a function of covariates. Our design procedure can thus be extended to provide designs for any extension to the basic SCR model that permits fast evaluation of $E(n)$ and $E(r)$. We illustrate this by developing designs incorporating non-uniform animal density and spatially-varying detection covariates. We show that the accuracy of the $CV(\hat{D})$ approximation remains good when density varies spatially, extending the results of previous simulations assuming constant density (Efford & Boulanger, 2019), and supporting the use of the approximation in this extended context.

Using the $CV(\hat{D})$ approximation as a design criterion relies heavily on the accuracy of the approximation not depending on detector configuration, except through the expected number of first captures and recaptures. We show that although designs that maximize approximate precision lead to greater sample sizes than regular grid designs, these gains are often offset by lower precision in other estimators, most notably those related to the effective area surveyed, which are not accounted for in the approximation. Nevertheless, $\min(n, r)$ designs are competitive with regular grid designs in most cases and sometimes outperform them, particularly when animal activity centre density varies spatially. They have the benefit of flexibility, being applicable to study regions of any shape, and can be expected to be easier and less costly to implement, owing to detectors being more clustered.

We illustrate the application of our proposed approach by revisiting a camera trap survey of snow leopards in the Tost Mountains of Mongolia. Using an existing survey provides a background context and plausible ranges for model parameters, and allows for comparison with actual design practices, all of which are useful for illustration and interpretability.

2 Materials and Methods

2.1 Components of the SCR model

Spatial capture-recapture (SCR) models comprise a spatial model of the population and a spatial model of the detection process. These are fitted jointly to the capture histories of detected individuals to provide estimates of, among other quantities, the density of individuals within an area, the effective area surveyed, and population size (Borchers & Efford, 2008; Royle et al., 2014).

The spatial model of the population describes the distribution of activity centres in the landscape, each animal represented by its activity centre. Locations of animal activity centres are assumed to be generated by a Poisson process with density ("intensity") $D(\mathbf{x})$ at a point $\mathbf{x}$ on a habitat mask A representing the survey region. The mask (or state space) is a two-dimensional polygon large enough that animals living outside the mask have a negligible chance of being detected, often obtained by adding a buffer region around detector locations. Density may be constant over space, corresponding to a random uniform distribution of animals in space, or may vary as a function of spatially-varying covariates. The number N of activity centres in A can either be treated as a Poisson random variable, in which case the number of activity centres N and their locations follows a Poisson point process, or as a single, fixed realization of that variable, in which case the activity centre locations follow a binomial point process. The approximation in (1) assumes a Poisson point process; for a binomal point process $CV(\hat{D}) \approx \sqrt{1/\min\{E(n), E(r)\} - 1/(DA)}$ (Efford & Boulanger, 2019). In what follows we assume a Poisson point process, but our approach is also applicable to the binomial case.

The detection process assumes a survey in which K detectors are placed in a region containing animals, each of which possesses an activity centre, for S survey occasions. The expected number of encounters of an individual whose activity centre is $\mathbf{x}$ at a particular detector k in occasion s is a decreasing function of the distance between the detector and the activity centre, $d_k(\mathbf{x})$. Various functional forms are assumed for this relationship, commonly a half-normal $\lambda(d_k(\mathbf{x})) = \lambda_0 \exp[-d_k(\mathbf{x})/(2\sigma^2)]$, where λ_0 is the cumulative encounter hazard for a detector at the centre of an animal's home range and σ is a scale parameter determining how quickly the encounter rate decreases with distance between detector and activity centre. Both parameters may also vary as a function of spatially-varying covariates measured at detector locations, although a more natural way to make σ depend on spatial covariates is almost always to model conductance of (or resistance to) movement as a function of spatial covariates, as in Sutherland, Fuller, and Royle (2015). The expected number of encounters over all detectors for an animal whose activity centre is $\mathbf{x}$ in occasion s is $\Lambda_s(\mathbf{x}) = \sum_k \lambda(d_k(\mathbf{x}))$ and over all occasions $\Lambda(\mathbf{x}) = \sum_s \Lambda_s(\mathbf{x})$. The effective sampling area covered by a survey is $a = \int_{\mathbf{x}} p_\cdot(\mathbf{x})\, d\mathbf{x}$, where $p_\cdot(\mathbf{x})$ is the probability that an animal with an activity centre at $\mathbf{x}$ is detected at least once during the survey. Conceptually, the effective sampling area downweights the area contribution of regions of the habitat mask where the detection probabilities $p_\cdot(\mathbf{x})$ are low.

Encounter data are collected as capture histories recording the presence of individual animals at detectors in each survey occasion. The exact format of the capture histories depends on the kind of detectors used. We use the same three used by Efford and Boulanger (2019), all of which assume that a detector can detect multiple animals at each occasion. Then, animals can be detected (a) at most once across all detectors in each occasion ("multi-catch traps"); (b) at most once at each detector in each occasion ("binary proximity detectors"); or (c) any number of times at each detector in each occasion ("count proximity detectors").

2.2 Design objectives

Royle et al. (2014) considered four design objectives – minimizing the trace of the variance-covariance matrix of the MLEs of detection model parameters; minimizing $\text{var}(\hat{\bar{p}})$, the variance of the MLE of the mean detection probability (the probability that an animal in A is detected by the survey); maximizing the mean detection probability; and minimizing $\text{var}(\hat{N}_c)$, where $\hat{N}_c = n/\hat{\bar{p}}$ is a conditional estimator of N and n is the number of animals detected – while Dupont et al. (2020) maximized $\bar{p}_m$, the mean probability that an animal is detected on two or more detectors. All except the fourth criterion in Royle et al. (2014) relate only indirectly to obtaining precise estimates of animal density or abundance. The fourth is an appealing design objective but cannot be calculated in closed form. Royle et al. (2014) provide an approximation, but this involves calculating all three of the other criteria as inputs, relies on asymptotic variance calculations that are only valid for Gaussian hazard detection models with Bernoulli observations, and approximates the variance-covariance matrix of the detection model parameter MLEs with the inverse of the expected Fisher information matrix under a standard Poisson GLM with fixed N.

Efford and Boulanger (2019) provide the much simpler approximation in (1), with expected numbers of first captures $E(n)$ and recaptures $E(r)$ given by

$$E(n) = \int_{\mathbf{x}} [1 - \exp(-\Lambda(\mathbf{x}))] D(\mathbf{x}) d\mathbf{x} \quad \text{(all detectors)} \tag{2}$$

and

$$E(r) = \int_{\mathbf{x}} \Lambda(\mathbf{x}) D(\mathbf{x}) d\mathbf{x} - E(n) \qquad \text{(count proximity detectors)} \tag{3}$$

$$E(r) = \int_{\mathbf{x}} \sum_{s=1}^{S} \sum_{k=1}^{K} [1 - \exp\{-\lambda(d_k(\boldsymbol{x}))\}] D(\mathbf{x}) d\mathbf{x} - E(n) \qquad \text{(binary proximity detectors)} \tag{4}$$

$$E(r) = \int_{\mathbf{x}} \sum_{s=1}^{S} [1 - \exp(-\Lambda_s(\boldsymbol{x}))] D(\mathbf{x}) d\mathbf{x} - E(n) \qquad \text{(multi-catch traps)} \tag{5}$$

Our approach can be applied to all three detector types, but for brevity we focus on count proximity detectors (eq. (3)) in the remainder of the paper. The approximation has no formal derivation but relies on two intuitions. The first is that natural variation in animal abundance sets an effective lower bound on how small $CV(\hat{D})$ can be, so that if the number of animals is assumed to be Poisson distributed with parameter n, as is commonly done, then this lower bound equals $1/\sqrt{n}$. The second is that recaptures decrease variance in $\hat{D}$. An exact relationship holds for a simple two-stage mark-recapture study. In that case, population size is estimated with the Lincoln-Petersen estimator $\hat{N} = n_1/(r/n_2)$ where n_1 and n_2 are number of captures at each visit and r is number of recaptured animals that were marked. The variance of this estimator is approximated by $1/r$ (Seber et al., 1982).

Simulations reported in Efford and Boulanger (2019) show that values of $CV(\hat{D})$ obtained by approximation closely matched those obtained by simulation across a number of problem settings assuming square arrays and uniform density of activity centres. For some detector geometries, the approximation underestimated $CV(\hat{D})$, in the case of linear detector arrays by 25%. Efford and Boulanger (2019) suggest that in such cases the approximation should be modified by a constant correction factor whose value is determined by simulation. To test whether the approximation also holds for heterogeneous density, we extended the same simulation experiment to include two spatially-varying density surfaces, one in which density was concentrated in the centre of the survey region, and one in which density increased with latitude and longitude, so that the highest densities were in the buffer region of the habitat mask, and assessed the quality of the approximation in these conditions (see Supplementary Material A for further details).

2.3 Optimization

Optimization requires the specification of potential camera locations, a convenient form for which is a grid of points over the survey region, excluding the buffer (Fig. 1a). A small spacing between potential detector locations provides greater flexibility for optimization, but spatial recaptures (detecting the same animal at different detectors) at very small distances provide little information about the shape of the detection function. Adequate spacing is crucial when optimizing any design criterion that treats all spatial recaptures as equivalent (e.g. $\min(n, r)$ and $\bar{p}_m$ designs) because the total number of spatial recaptures is maximized by placing detectors as close together as is allowed by the spacing. This reduces spatial coverage (and thus, n) and leads to many recaptures at relatively uninformative fractions of σ, both of which serve to inflate the

CV of the effective sampling area a. Guidelines from simulations with square grids (Efford and Boulanger (2019), also our Fig. 2) cannot be applied directly to the choice of spacing of *possible* detector locations, but suggest a minimum spacing no less than $\sigma/2$. We used a slightly more conservative spacing of $2\sigma/3$.

Selecting a design minimizing (1) involves a difficult combinatorial optimization problem for which exact methods are not available. The solution space consists of all $\binom{M}{K}$ possible ways of allocating K detectors across a discretized grid of M possible locations. This is typically an enormous number (with 500 possible locations and 50 cameras, there are 10^{69} possible designs), precluding enumeration; in addition the objective function is non-linear. Various stochastic or approximate solution methods might be used. We initially used a modified Federov algorithm as implemented in Royle et al. (2014), but these tended to produce isolated small clusters of detectors that can be expected to be biased (Clark, 2019) and for which $CV(\hat{D})$ was poorly approximated (Fig. 1c). We then used a standard genetic algorithm implemented in the R package `kofnGA` (Wolters, 2015), following Dupont et al. (2020), that is much less susceptible to this problem (Fig. 1e). The algorithm begins by generating a population of random designs, typically several hundred. These are evaluated using the design criterion, with good designs selected preferentially and with replacement. Selected designs are randomly paired, and each design in a pair exchanges some proportion of its locations with its partner to create two new designs. A final mutation step potentially replaces, with a small probability, each location with a randomly selected one. Over all pairs, these new designs constitute the next population, which again undergoes selection, location exchange, and mutation. The process continues for a fixed number of iterations or until convergence is achieved.

As the optimization relies only on expected values of n and r, it has no inbuilt way of avoiding "pathological" designs (Efford & Boulanger, 2019) in which detectors cover too small an area, or are spaced too far apart, for reliable and unbiased estimates of SCR model parameters. To prevent the optimizer straying toward, or selecting, these designs, we added a large penalty term to the objective function in (1), incurred by any designs that do not satisfy some pre-defined desirable criteria. Since these are mainly used to rule out undesirable designs, various criteria are possible (Efford & Boulanger, 2019). We constrained designs to have at least as many detectors separated by 2.5-3.5σ and 3.5-4.5σ as a regular 2σ grid, to encourage reliable estimation of σ (Fig. 1).

2.4 Case study: camera trap survey of snow leopards in Tost, Mongolia

The Tost Mountains are a rugged mountain range occupying an area of $\sim$2100km^2 and are separated from nearby ranges by several kilometers of steppe that discourage snow leopard movement between ranges, so that in previous analyses the area has been treated as closed. Camera trap surveys have been conducted since 2009 as part of long-term snow leopard monitoring projects (K. Sharma et al., 2014). Snow leopards have large home ranges of 80-700 km^2 in size (Johansson, Simms, & McCarthy, 2016) and this, together with difficult terrain and harsh environments, have historically made assessment challenging and only amenable to camera trap surveys, of which a fairly large number have been carried out (e.g. Alexander, Gopalaswamy, Shi, & Riordan, 2015; McCarthy et al., 2008; K. Sharma et al., 2014; R. K. Sharma, Bhatnagar, & Mishra, 2015).

A camera trap survey of Tost conducted in 2012 (K. Sharma et al., 2014) collected 14 first captures and 40 recaptures using an array of 40 camera traps, placed predominantly in areas of rugged terrain (Supplementary Material B). Potential locations for placing cameras were subjectively identified by regional experts based on landscape features suggesting broadly favourable snow leopard habitat. Camera trap locations were identified by surveying 2-5 km on foot in the mountains around each potential location and searching for fresh snow leopard signs (scrapes, urine markings) or, in the absence of such markings, favourable features such as paths along ridgelines, overhanging rocks or steep canyon walls. Emphasis was thus on selecting broad areas, and precise camera locations, where the possibility of capturing snow leopards was high. Cameras were typically tightly spaced, with 25% of cameras being within 2km of another

Figure 1: Illustration of optimizing SCR design; (a) potential detector locations with spacing $\sigma/2$; designs selected by (b) a modified Federov algorithm, (c) a modified Federov algorithm with additional constraints on detector spacing, (d) a genetic algorithm, which returns the same design with or without constraints, (e) a typical grid design with 2σ spacing. Designs (b), (c), and (d) all have $E(n) = E(r) = 62.8$, and thus expected $CV(\hat{D}) = 12.6\%$, but simulated $CV(\hat{D})$'s are 30, 15.8, and 16.5%. The design in (b) suffers from inadequate spacing and cluster size, which inflates $CV(\hat{a})$ (27, 9, and 9% respectively). The modified Fedorov algorithm tends towards these designs unless constrained, while a genetic algorithm does not. A regular grid design gives fewer recaptures ($E(n) = 71$, $E(r) = 48$) and hence has a higher approximate $CV(\hat{D}) = 14.4\%$. Despite this, its simulated $CV(\hat{D}) = 15.8\%$ is at least as good as optimized designs, because of more precise estimates of $CV(\hat{a}) = 8\%$ not accounted for in the approximation.

camera and 70% of cameras within 4km. Cameras were left in the field for an average of 105.45 (SE=11.81) days and took 7-20 days to set up.

We first generated min(n, r) designs[1] for the survey region under the assumption of constant animal activity centre density across the survey region and setting values for SCR model parameters that allowed us to cover the entire area with a regular grid of 60 detectors spaced 2σ apart, while returning expected sample sizes broadly similar to those observed in the real study (20 individuals detected and 24 recaptures, using actual camera locations). We set the activity centre density at 2/100 km^2, towards the higher end of known snow leopard density estimates. Importantly, detector locations in min(n, r) designs are unaffected by changes in mean animal density, which simply changes the numbers of first captures and recaptures proportionately. The same configurations of detectors (for example, those reported in Fig. 3) would be obtained for any choice of mean activity centre density, although these may result in very different values of $CV(\hat{D})$. All min(n, r) designs were generated using the genetic algorithm described in the previous section. We used 50 generations (designs typically converged considerably earlier than this), a population size of 1000 and a mutation rate of 1%.

Detection function parameters were set to $\sigma = 3$km and encounter rate $\lambda_0 = 1$, again on the basis of ballpark similarity to previous studies and to provide roughly the desired number of first captures and recaptures. A buffer of 3σ was used with a spacing of $2\sigma/3 = 2$km between mask points (or, equivalently, the centroids of mask cells). Potential camera locations were specified using a grid of points with the same spacing used in the habitat mask.

For this "baseline" case we generated min(n, r) designs for 20-, 40-, and 60-camera arrays. Cameras were treated as count proximity detectors, except in one set of results where we assessed the effect of detector type. For each design we report and discuss differences in the expected number of first captures $E(n)$, recaptures $E(r)$, approximate CV, and detector locations. We then varied SCR model parameters one at a time, and generated further sets of survey designs.

[1] All code and output are available at `https://github.com/iandurbach/optimal-secr-design`.

We changed λ_0 and σ to 50%, 150%, and 200% of their baseline values of $\lambda_0 = 1$ and $\sigma = 3$, and changed the buffer from a baseline of 3σ to zero to simulate the treatment of the survey region as closed, as had been assumed in previous analyses.

We then generated designs for three extensions to the basic SCR model: one with spatial covariate on density, one with a spatial covariate on detectability, and one with spatial covariates on both density and detectability. Designs for a model with spatially-varying density assumed that expected animal activity density depended on a standardized terrain ruggedness index i.e. $D(\mathbf{x}) = \exp(\alpha_{0D} + \alpha_D R(\mathbf{x}))$, where $R(\mathbf{x})$ is the value of the ruggedness covariate at $\mathbf{x}$ and α_{0D} is chosen so that mean animal density across the study area is the same as in the uniform density case. For this set of designs we jointly varied the size of the array (20, 40, or 60 cameras) and the relationship between density and ruggedness ($\alpha_D \in \{-1, 1, 3\}$), with other parameters held fixed at their baseline values ($\lambda_0 = 1$, $\sigma = 3$, 3σ buffer).

Optimal designs for a model with spatially-varying detector covariates assumed that expected encounter rate depended on longitude i.e. $\lambda_0(\mathbf{x}) = \exp(\alpha_{0\lambda_0} + \alpha_{\lambda_0} x_1)$, where x_1 is the longitudinal component of $\mathbf{x}$. We jointly varied the size of the array (20, 40, or 60 cameras) and the relationship between baseline encounter rate and longitude ($\alpha_{\lambda_0} \in \{-0.75, 0.75, 1.5\}$), with other parameters held fixed at baseline values. Where animal density was uniform we used the baseline value $D = 2/100$ km^2; where both density and detectability varied spatially we used $\alpha_D = 1$ and $\alpha_{\lambda_0} \in \{-0.75, 0.75, 1.5\}$.

We generated sets of designs using two other approaches, again recording $E(n)$, $E(r)$, approximate and simulated CV, detector locations, and between-detector spacings for each design. The first uses a regular grid of detectors with 2σ spacing between traps. We generated a regular grid of K detectors by creating a grid covering the survey region and choosing a subset of K points – an initial grid point and its $K - 1$ nearest neighbours. The initial grid point was chosen randomly when detection was uniform, at the point of highest density or detectability when either these varied spatially, and at the point of highest density when both varied. This encourages a square grid as far as permitted by the irregular survey area and starting point, and places the array in sensible parts of the survey region.

The second approach uses a regular grid with detector spacing chosen to minimize approximate $CV(\hat{D})$, using the *optimalSpacing* function in the `secrdesign` package (Efford, 2019b). This calculates $E(n)$ and $E(r)$ at various detector spacings and finds the optimal spacing by linear interpolation. We calculated the optimal spacing for each unoptimized grid generated by the first method, and then generated a new grid of detectors using the same process as before. Where the optimal spacing was too large to place the desired number of cameras in the survey region, it was set to the largest spacing that would allow the cameras to be placed.

For each scenario and design, we compared approximate CV to an empirical estimate of $CV(\hat{D})$ obtained from simulation. In each case, we simulated 1000 animal populations and associated capture histories, fitted an appropriate SCR model to each capture history, and calculated the CV of the fitted density estimates. Simulated populations, capture histories, and fitted models included spatially-varying density and detection in those scenarios that made use of them. Models were fitted using the R package `secr` (Efford, 2020).

3 Results

3.1 Approximation accuracy

The approximation of $CV(\hat{D})$ was slightly less accurate when density varied spatially but remained broadly reliable (Fig. 2). Underestimation of $CV(\hat{D})$ occurred with small detector spacing (0.25σ), and this underestimation was more severe for one of two non-uniform density scenarios. With detector spacing of $< 1\sigma$, the approximation remained good so long as approximate $CV(\hat{D}) < 20\%$ when density was uniform, with a stricter condition approximate $CV(\hat{D}) < 15\%$ if density varied spatially. Approximation accuracy was relatively poor for a scenario where density increased with latitude and longitude, because the highest-density areas were part of the buffer region of the habitat mask and not accessible to detectors. Although not practically likely, this demonstrates that the approximation is somewhat sensitive to the density surface when this varies spatially.

3.2 Designs under uniform animal density and habitat use

In the baseline scenario, with only 20 detectors, recaptures were the limiting factor and so detectors were placed close together (Fig. 3a). As detectors were added spacing between cameras increased to detect more animals, until a spatially well-balanced arrangement broadly resembling a space-filling design was obtained (Fig. 3c).

Restarting the optimization process from different starting points led to different designs that for the most part shared the same aggregate properties (Fig. 3d-f; Supplementary material C). When animal density is assumed uniform, it makes little difference exactly where a camera is located, as long as aggregate properties such as detector spacing are preserved. Visible differences between the two designs were greatest in the 20-detector case, but both designs returned very similar approximate $CV(\hat{D})$'s (Table 1).

In reality the Tost survey region is closed due to boundaries of steppe that snow leopards avoid. We therefore simulated a scenario with no buffer region (Fig. 3g-i). Shrinking the buffer to zero pulled traps away from the border and towards the centre of the study area, because detectors at or near the border would include areas of known absence in their detection range and thus be inefficient.

Changing the encounter rate intercept parameter λ_0 or the scaling parameter σ had a similar effect (Fig. 3j-l for λ_0, m-o for σ). Decreasing either of these lowered the frequency of recaptures and so caused detectors to be more concentrated (Fig. 3j,m). Increases had the opposite effect, causing detectors to be more spread out (Fig. 3k and n). Large values of σ resulted in many detectors being placed along the boundary of the survey area, with relatively few detectors in the interior (Fig. 3n,o).

Designs for binary proximity detectors and especially multi-catch traps tend to be more clustered together than count proximity detectors, given the same background conditions (Fig. 3p-r). This happens because binary proximity detectors treat multiple detections of the same

Figure 2: Approximation of precision of $CV(\hat{D})$ (solid lines, circles) compared to simulated precision (dashed lines, triangles) for square grids over a range of detector spacings for (a) uniform density of activity centres, (b) density concentrated in the centre of survey region, decreasing with distance from centre (c) density increasing with latitude and longitude, so that the highest densities are in the buffer of the habitat mask. Experimental setup is as for Efford and Boulanger (2019) except that density varies spatially. See Supplementary Material A for further details and results. Approximation accuracy is less robust when density varies spatially but remains broadly reliable.

Figure 3: Examples of $\min(n, r)$ survey designs for an SCR survey of snow leopards in Tost, Mongolia. All plots assume uniform activity centre density across the survey region. Grid cells are 2×2km and detectors are indicated in red. "Baseline" conditions refer to setting $\lambda_0 = 1$ and $\sigma = 3$, with a 3σ buffer. These and the number of detectors are independently varied in the sub-plots to demonstrate how optimal designs respond to changes in input parameters.

Scen	CV($\hat{D}$) (actual) Min	Grid	G+O	CV($\hat{D}$) (approx) Min	Grid	G+O	CV($\hat{a}$) Min	Grid	Gr+O
Effect of varying number of detectors									
(a)	60	61	47	30	33	31	32	25	22
(b)	27	24	24	21	23	22	16	14	11
(c)	20	19	20	17	18	18	11	11	8
Effect of random starts									
(d)	57	50	46	30	33	31	28	23	22
(e)	25	24	24	21	23	22	15	14	12
(f)	20	19	19	17	18	18	12	11	8
Effect of zero buffer									
(g)	58	63	44	30	34	34	29	25	22
(h)	26	25	24	21	23	24	16	13	12
(i)	20	20	20	18	19	20	11	11	8
Effect of varying encounter rate λ_0									
(j)	30	44	28	24	33	26	17	25	13
(k)	16	16	16	14	15	15	8	7	6
(l)	15	14	15	14	14	15	7	5	4
Effect of varying movement parameter σ									
(m)	149	88	49	39	36	36	35	26	20
(n)	13	13	14	12	13	13	7	5	4
(o)	11	12	12	10	11	12	4	4	4
Effect of detector type									
(p)	21	21	22	19	22	21	9	12	8
(q)	20	19	20	18	20	19	11	10	7
(r)	21	19	19	17	18	18	12	10	7

Table 1: Comparing approximations of $CV(\hat{D})$ (col. 4-6) with values obtained by simulation (col. 1-3), for each of the scenarios in Fig. 3. Min = $\min(n, r)$ designs; Grid = regular grid designs with 2σ spacing; G + O = regular grid designs with optimal spacing; see Section 2.4 for details. Approximate and simulated values are close when $CV(\hat{D}) < 20\%$. Optimized $\min(n, r)$ designs provide more first captures and recaptures than grid designs, but can still have lower (simulated) precision because their effective sampling areas are less precisely estimated ($CV(\hat{a})$, col. 7-9).

density. As a result, $\min(n, r)$ designs remained better than regular 2σ grids in most scenarios involving spatially-varying density, although again usually only by a small margin. Substantial improvements were achieved in some scenarios where areas of high density and high detectability differered substantially (Fig. 4h,i). These scenarios are not biologically plausible but illustrate some of the potential drawbacks of regular designs in more complex environments.

Detectors were more concentrated when covariate relationships were stronger (cf. Fig. 4, b,e,h vs. c,f,i), but the increase was not extreme. The incentive of detecting new individuals encouraged clusters of detectors to form away from high-density or high-detectability areas, once these areas had been exploited. Detector locations spanned the majority of the covariate space, even in quite extreme scenarios (Fig. 5). Good coverage of covariate space is important because unbiased estimates of density depend on covariate relationships being accurately estimated, and this is much more likely if the covariate space has been well sampled.

Covariate coverage is not part of the objective function, and so not something that is under direct control of the optimizer. In our application covariate coverage was better when the density-ruggedness relationship was positive than when it was negative, because cells with high ruggedness were concentrated in one area while cells with low ruggedness were dispersed throughout the survey region. In the latter case, it was possible for clusters to be located so that they were far from one another *and* occupied areas of high density (low ruggedness). When the relationship was positive this was not possible. This means that covariate coverage should always be assessed, for example using rug plots such as Fig. 5.

Figure 4: Designs for scenarios involving spatially-varying density ($D(\mathbf{x})$) or detectability ($\lambda_0(\mathbf{x})$). Activity centre density depends on terrain ruggedness. Baseline encounter rates depend inversely on longitude (highest in west), with activity centre density either uniform (d-f) or also varying spatially (g-i). Panel labels give covariate coefficients, indicating the direction of the assumed relationship. Grid cell colour indicates terrain ruggedness (a-c, g-i), with lighter colours denoting higher values, or longitude values (d-f). Detectors are placed preferentially where density or detectability is expected to be highest in order to maximize the number of animals detected. However, because recaptures must also be considered, concentration of detectors in high density or detection areas is generally not extreme.

Figure 5: Coverage of spatially-varying density and detectability covariates by $\min(n, r)$ designs. Points plot covariate values at the detector locations in Fig. 4a-f, with the curve showing the functional form of the assumed relationship between density and ruggedness. Coverage is better for positive values of α_D in our case study because the method initially places detectors in high-density patches, before spreading into lower-density patches.

	CV($\hat{D}$) (actual)			CV($\hat{D}$) (approx)			CV($\hat{a}$)		
Scen	Min	Grid	G+O	Min	Grid	G+O	Min	Grid	Gr+O
Designs with spatially-varying density									
(a)	25	24	30	19	22	21	12	11	6
(b)	19	20	20	17	19	18	7	8	5
(c)	15	19	15	15	16	15	3	8	4
Designs with spatially-varying detection									
(d)	24	22	25	20	21	24	12	8	3
(e)	23	21	40	21	21	25	11	10	4
(f)	23	22	35	22	23	25	8	9	3
Designs with spatially-varying density and detection									
(g)	18	19	19	16	17	18	7	6	5
(h)	24	36	25	18	32	23	14	21	13
(i)	41	62	54	23	76	52	30	41	36

Table 2: Comparing approximations of $CV(\hat{D})$ (col. 4-6) with values obtained by simulation (col. 1-3), for each of the scenarios in Fig. 4. Min = $\min(n, r)$ designs; Grid = regular grid designs with 2σ spacing; G + O = regular grid designs with optimal spacing; see Section 2.4 for details. In contrast to uniform scenarios, optimized designs have higher (simulated) precision than grid designs in scenarios where their effective sampling areas are estimated with similar precision ($CV(\hat{a})$, col. 7-9).

4 Discussion

The optimization of approximate $CV(\hat{D})$ provides statistically grounded guidance on selecting detector locations for SCR surveys. The way in which designs change in response to changes in survey variables (the number of cameras available) or exogenous variables (encounter rate, animal density, movement, buffer size) represents the best available balance between the competing objectives of maximizing the number of animals detected and maximizing the number of recaptures. Designs generated in this way are transparent and objective. They can be adapted for survey regions of any shape, adapt to known information about animal density, detectability, and movement, and are generally more clusterered designs that may be easier and less costly to implement than standard grid designs.

The current approximation of $CV(\hat{D})$ is highly accurate when $CV(\hat{D}) < 15\%$ under both uniform and non-uniform animal density, and remains within a few percent of simulated values so long as $CV(\hat{D}) < 20\%$. However, any discrepency almost always overestimates precision, and by a slightly larger margin for irregular detector arrays than for regular one. This reduces the gains provided by optimizing $\min\{E(n), E(r)\}$ and in our scenarios involving uniform animal density was often sufficient to reverse it, although differences between optimized and regular grid designs were small in all scenarios except near-pathological ones. The $CV(\hat{D})$ of optimized designs can be worse than that of regular 2σ designs, even if they result in more first captures and recaptures, because the effective sampling area of these designs is generally smaller and less precisely estimated, owing to less precise estimates of detection function parameters, particularly σ, that are not accounted for in the approximation. Other approaches that optimize simple functions of sample size or detection probability are likely to face similar challenges. Further investigation may lead to improvements in the approximation but, until then, $\min(n, r)$ designs should not be considered optimal, but rather good, flexible candidate designs to be compared with other designs using simulation.

Other factors known to cause poor approximation accuracy are small detector spacing, "pathological designs" in which detectors cover too small an area, or are spaced too far apart, and linear detector arrays (Efford & Boulanger, 2019). Small detector spacings appear attractive because they provide greater flexibility for optimization and generally offer more recaptures, but spatial recaptures at very small distances provide little information on σ, and this ultimately negatively affects $CV(\hat{D})$. We suggest a minimum spacing no less than $\sigma/2$. Narrower spacing may very occasionally be warranted for species that are nearly impossible to recapture (**?**, e.g.), although in these cases serious consideration should be given as to whether the data collected will be adequate for the use of SCR. Pathological designs can be removed from consideration by heavily penalizing any designs that do not satisfy some pre-defined criteria. Since these are used only to rule out undesirable designs, various criteria are possible (Efford & Boulanger, 2019). For example, we constrained designs to have at least as many detectors separated by 2.5-3.5σ and 3.5-4.5σ as a regular 2σ grid. Linearity of detectors can in principle be assessed and corrected for at each step of the optimization process, but currently the only way to do this is with computationally intensive simulation that renders optimization impractical. One possibility is to summarize the linearity of an irregular array in a way that allows the correction factor in Efford and Boulanger (2019) to be inferred in a meaningful and computationally feasible way, but we have not pursued this here. Very few of our designs exhibited signs of linearity. Using simulation to carry out *post hoc* checks of $CV(\hat{D})$, with minor manual adjustments to detector placements to break linear arrangements where necessary (also guided by simulation), is probably sufficient in the majority of cases.

The precision of density estimates appears to be robust over a wide range of detector placements, so long as problems of pathological designs are avoided. Regular designs return $CV(\hat{D})$'s within a few percent of each other over a wide variety of detector spacings (Efford and Boulanger (2019), Fig. 2) and our designs were in turn almost always within a few percent of these. Regular 2σ designs provide an excellent, robust default design. The primary benefit of $\min(n, r)$ designs is that they lead to estimators with comparable precision to the best currently available alternatives, while being applicable to any survey region and with the potential to incorporate information about animal behaviour that may in some cases improve precision. Large improvements in precision, however, are probably achievable only by using more detectors or increasing survey duration in the majority of cases. Better choices of detector locations will not be able to remedy fundamental deficiencies in animal density or detection rates.

Designs that maximize the precision of density estimators without accounting for the possibility of bias run the risk of returning biased estimates of density. If this bias is substantial it may outweigh any gains made by reducing variance. Bias is unlikely to be a problem when activity centres are assumed to be uniformly distributed, as several studies have demonstrated that a variety of SCR surveys are unbiased under these conditions (Efford, 2019a; Efford & Boulanger, 2019; Sun et al., 2014). We assessed the bias of each of our designs including spatially-varying density and detection (those in Fig. 4) using simulation (see Supplementary Material D for details), and results indicated that these designs returned estimates of density that exhibited little or no bias. We recommend that designs assuming spatially-varying covariates always include a *post hoc* assessment of the coverage of covariates, as well as *post hoc* assessments of possible bias. If the optimized design does not achieve good coverage, we recommend reverting back to simpler designs with regular spacing, or manually adjusting detector locations to improve covariate coverage, followed by a reassessment of $CV(\hat{D})$. It is also possible to build covariate coverage into the optimization as an objective in its own right, although we have not explored this here.

Optimal designs place detectors in locations that exploit particular features of animal density and detectability, represented by parameters like λ_0, σ, and coefficients for any spatial dependencies. While our approach extends to a number of more advanced SCR variants, these will require reasonable knowledge about the parameters of those models, which may only rarely be available before the survey is conducted. Many SCR surveys are designed with little or no knowledge of what values these parameters might take on, and optimized designs may be expected to perform worse than regular designs if parameter values are poorly chosen. We have not investigated this issue in detail for all parameters, but recalculated the approximate $CV(\hat{D})$ of all designs using values of λ_0, σ, or α_1 up to 50% smaller (or 50% larger) than the values used to generate the designs. The approximate CV of $\min(n, r)$ designs remained better than any other candidate designs for almost all conditions (Supplementary Material E). Still, we recommend that optimized designs for any SCR variant only be used where there is good existing knowledge on the possible values of all the parameters of the model, and that simpler designs be used otherwise. In cases where knowledge extends only to σ, an optimal design is inappropriate and a regular-spaced design should be used.

Our designs take no account of the cost, monetary or other, of implementing a particular design, and so may end up choosing a costly design on the basis of a small improvement in approximate precision. However, in our scenarios $\min(n, r)$ designs had smaller average spacing between detectors, were more clustered, and had shorter shortest paths through the detector array (Supplementary Material C), all of which suggest lower cost and easier implementation.

Design costs can be incorporated into the optimization process, either by rejecting or penalizing costly designs or by including cost minimization as a second objective, but we leave this to future work.

5 Conclusion

This paper presents an approach for choosing detector locations in SCR surveys so as to maximize the expected precision of density estimates obtained from the later survey. The approach essentially combines the optimization framework used by Dupont et al. (2020), which employs a genetic algorithm to iterately improve candidate designs, with a new objective function using Efford and Boulanger (2019)'s approximation of the (standardized) precision of density, $CV(\hat{D})$. Our approach can in principle be extended to any variant of SCR for which $E(n)$ and $E(r)$ can be rapidly evaluated. Software for constructing $\min(n, r)$ survey designs has been developed based on a modification of the design function *Enrm* in the R package `secrdesign`, which provides a fast C implemention of $E(n)$ and $E(r)$ (see Supplementary Material F for details, and Supplementary Material G for a minimal working example). Optimization typically takes no more than a few minutes, even for quite large survey regions.

The main benefits provided by $\min(n, r)$ designs are a transparent process that reduces the need for difficult and subjective design decisions, for example around detector spacing and clustering, flexibility with respect to survey region, the ability to include environmental covariates affecting density, detectability, and movement. Gains in precision are possible with $\min(n, r)$ designs, but these are typically modest and occur where precision is already high ($CV(\hat{D}) < 15\%$). Usually, the precision of optimized and regular grids are within a few percent of one another. There seems relatively little downside to including a $\min(n, r)$ design in the candidate set of designs when planning an SCR survey. Simulation is essential as a means of confirming the $CV(\hat{D})$ of any design before final implementation (Efford & Boulanger, 2019).

Optimal designs for SCR surveys have received very little attention, which is surprising given the popularity of SCR and the cost and effort involved in conducting many surveys. Our paper develops optimized designs based on an intuitive and statistically grounded criterion, but also raises a number of questions deserving further attention. These include developing a better understanding of the origins of the approximation; potential improvements to the approximation; more comprehensive comparisons of optimal and other design protocols; sensitivity analyses to misspecification of initial parameter values; designs accounting for individual-level (e.g. sex-specific) detection covariates; inclusion of design costs; and optimization of survey duration as well as location.

Acknowledgements

This work was done to support the Population Assessment of the World's Snow Leopards (PAWS) initiative being coordinated by the Global Snow Leopard and Ecosystem Protection Program (GSLEP) through funding from the Global Environment Facility (Trans-boundary co-operation for snow leopard and ecosystem conservation project ID 5886), made available through United Nations Development Program and International Snow Leopard Trust. ID is supported in part by funding from the National Research Foundation of South Africa (Grant ID 90782, 105782). We are grateful to the two anonymous reviewers for their detailed and helpful comments, which led to a substantially improved manuscript.

Data Availability

All code and output are available at `https://doi.org/10.5281/zenodo.4074086` (Durbach, Borchers, Sutherland, & Sharma, 2020). This provides a permanent link to the version of the repository `https://github.com/iandurbach/optimal-secr-design` used to generate the results in this paper.

Authors' contributions

All authors conceived the work. DB, ID and CS designed the methodology. KS provided input on snow leopard survey design, data on existing designs, and feedback on proposed designs. ID performed the simulations and wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

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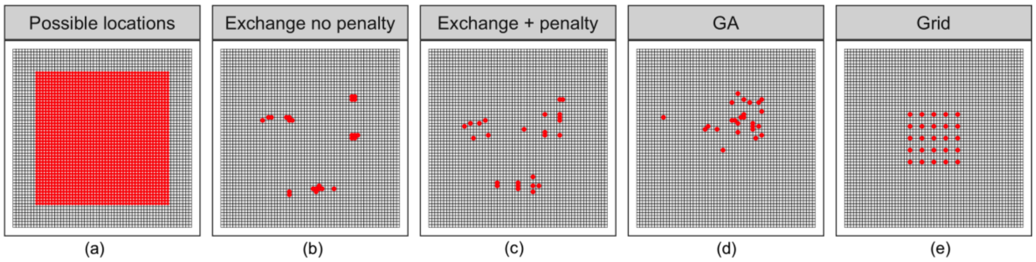
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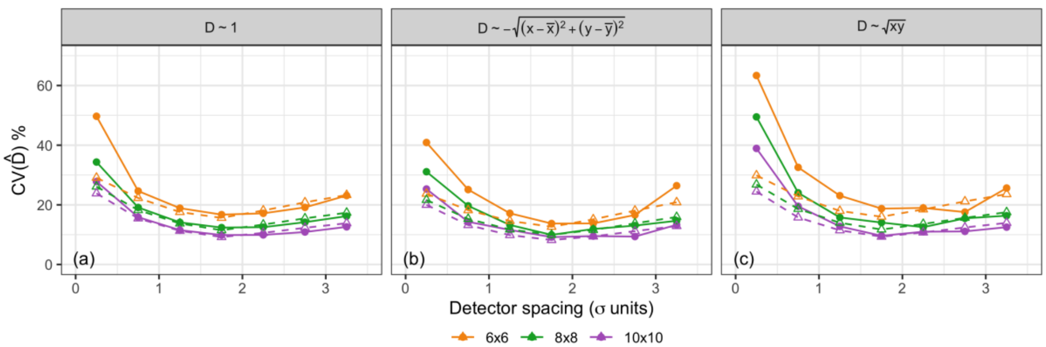

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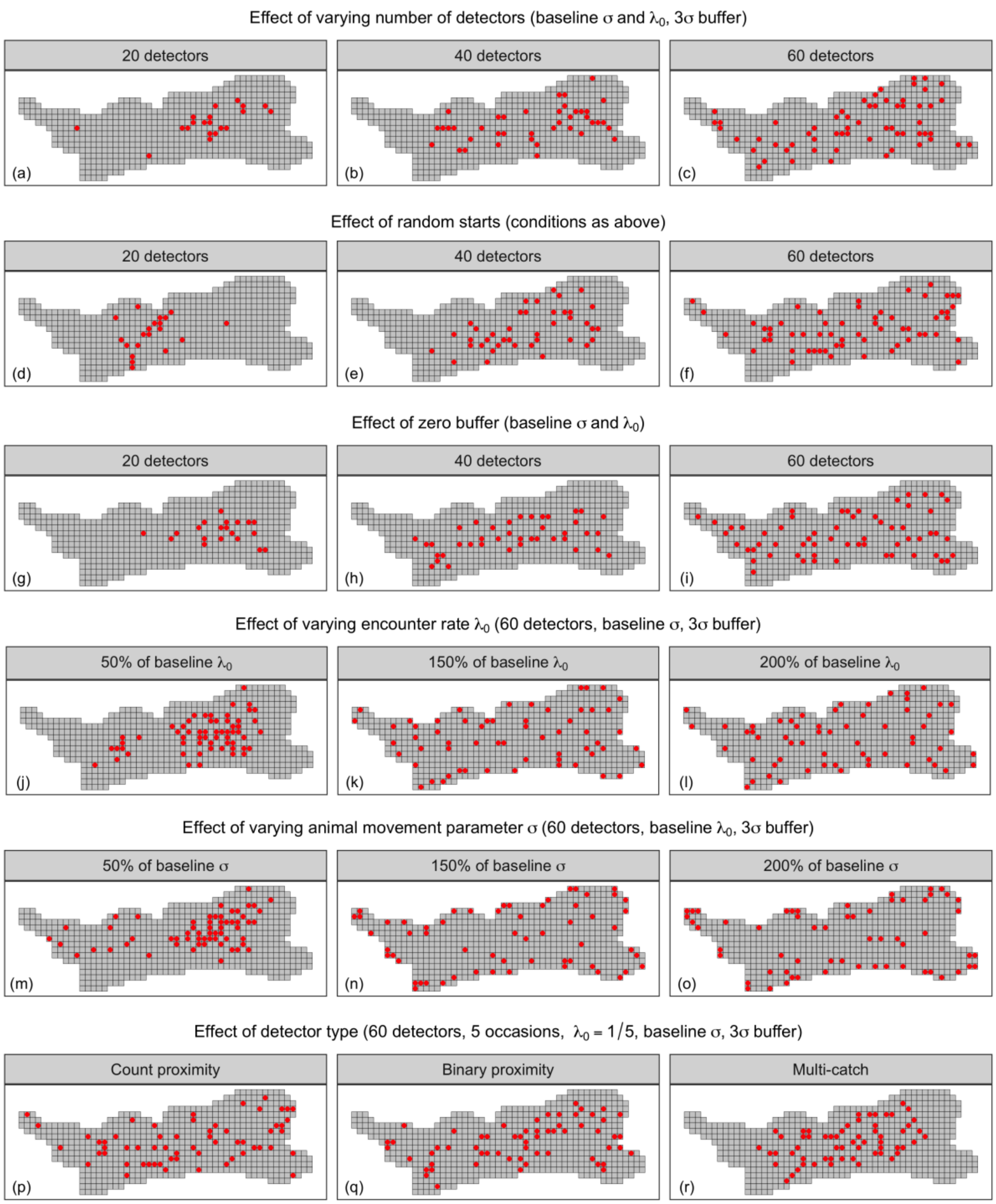

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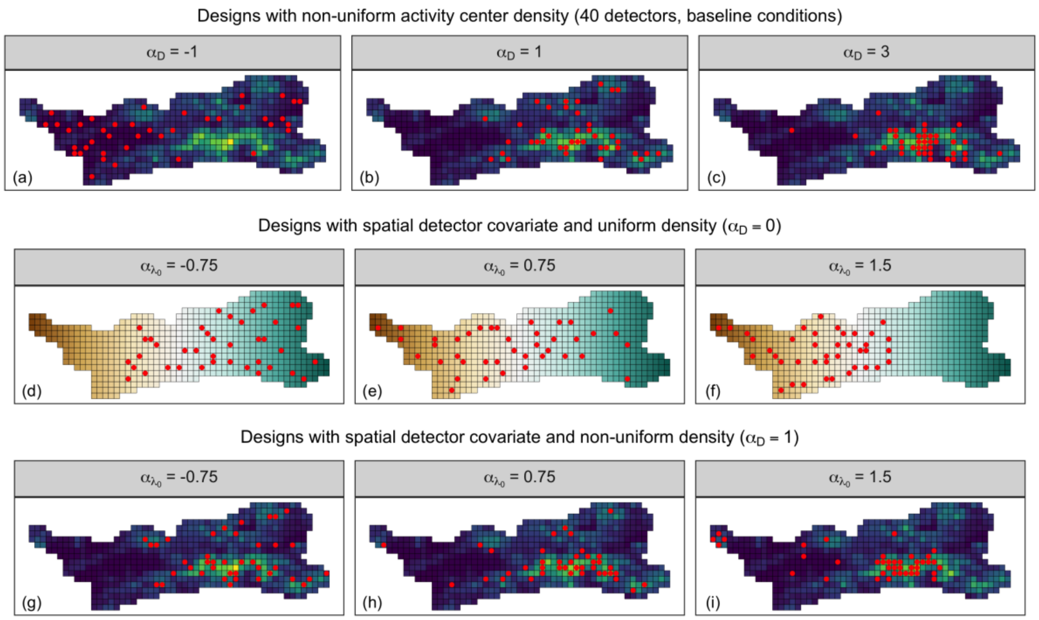

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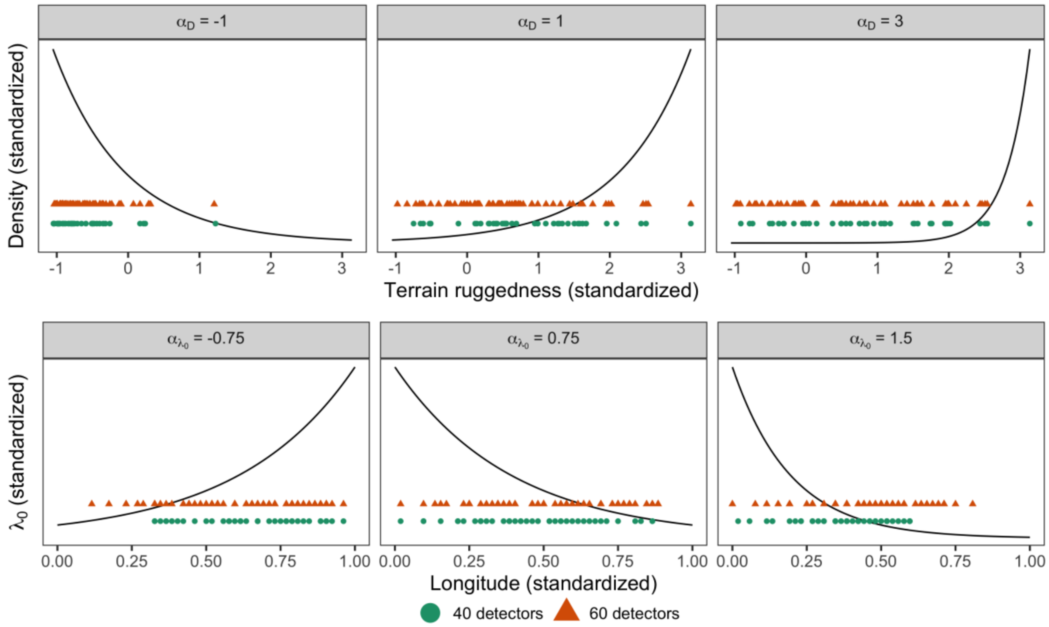

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