

Sampling Design

10

Statistical design is recognized as an important component of animal population studies (Morrison et al., 2008; Williams et al., 2002). Many biologists have been in a situation where some problem with their data could be traced back to a flaw in study design. Commonly, design is thought of in terms of number of samples to take, when to sample, methods of capture, desired sample size (of individuals), power of tests, and related considerations. In the context of spatial sampling problems, where populations of mobile animals are sampled by an array of traps or devices, there are a number of critical design elements. Two of the most important ones are the spacing and configuration of traps (or sampling devices) within the array. For traditional capture-recapture (CR), conceptual and heuristic design considerations have been addressed by a number of authors (e.g., Nichols and Karanth, 2002, Chapter 11), but little formal analysis focused on spatial design of arrays has been carried out. Bondrup-Nielsen (1983) investigated the effect of trapping grid size (relative to animal home range area) on capture-recapture density estimates using a simulation study and some authors have addressed trap spacing and configuration by sensitivity “re-analysis” (deleting traps and reanalyzing; Wegge et al., 2004; Tobler et al., 2008). The scarcity of simulation-based studies looking at study design issues is surprising, as it seems natural to evaluate prescribed designs by Monte Carlo simulation in terms of their accuracy and precision. In the past few years, however, a growing number of simulation studies addressing questions of study design in the context of spatial capture-recapture (SCR) have been published (e.g., Marques et al., 2011; Sollmann et al., 2012; Efford and Fewster, 2012; Efford, 2011b), the results of which we will discuss throughout this chapter.

In this chapter we recommend a general framework for evaluating design choices for SCR studies using Monte Carlo simulation of specific design scenarios based on trade-offs between available effort, funding, logistics, and other practical considerations—what we call *scenario analysis*. Many study design-related issues can be addressed with preliminary field studies that will give you an idea of how much data you can expect to collect with a unit of effort (a camera trap day or a point count survey, for example). But it is also always useful to perform scenario analysis based on simulation before conducting the actual field survey not only to evaluate the design in terms of its ability to generate useful estimates, but also so that you have an expectation of what the data will look like as they are being collected. This gives you the ability to recognize some pathologies and possibly intervene to resolve issues before they render a whole study worthless. Suppose you design a study to

place 40 camera traps based on expectations of parameter values you obtained from a careful review of the literature, and simulation studies suggest that you should get 3–5 captures of individuals per night of sampling. In the field you find that you’re realizing 0 or 1 captures per night and therefore you have the ability to sit down and immediately question your initial assumptions and possibly take some remedial action in order to salvage your project, your PhD thesis or even your career. Simulation evaluation of design *a priori* is therefore a critical element of any field study.

While we recommend scenario analysis as a general tool to understand your *expected data* before carrying out a spatial capture-recapture study, it is possible to develop some heuristics and even analytic results related to the broader problem of model-based spatial design (Müller, 2007) using an explicit objective function based on the inference objective. We outline an approach in this chapter where we identify a variance criterion, namely, the variance of an estimator of N for the prescribed state-space. We show that this depends on the configuration of trap locations, and we provide a framework for optimizing the variance criterion over the design space (the collection of all possible designs of a given size). While there is much work to be done on developing this idea, we believe that it provides a general solution to any type of design problem where the space of candidate trap locations is well defined.

10.1 General considerations

Many biologists have experience with the design of natural resource surveys from a classical perspective (Thompson, 2002; Cochran, 2007), a key feature of which involves sampling space. That is, we identify a sample frame comprised of spatial units and we sample those units randomly (or by some other method, such as generalized random tessellation stratified (GRTS) sampling (Stevens and Olsen, 2004)) and measure some attribute. The resulting inference applies to the attribute of the sample frame. There are some distinct aspects of the design of SCR studies which many people struggle with in their attempts to reconcile SCR design with classical survey design problems. We discuss some of these here.

10.1.1 Model-based not design-based

Inference in classical finite-population sampling is usually justified by “design-based” arguments. This means that properties of estimators (bias, variance) are induced by the method of sampling, and they are evaluated by averaging over realizations of the *sample*. The sample is random, but the attribute being observed is not, for the specific sample that is chosen. For example, imagine we have a landscape gridded off into 900 1 km × 1 km grid cells, from which we draw a sample of 100 to measure an attribute such as “percent developed” which we aim to use in a habitat model. In the classical design-based view, the attribute (percent developed) is a static quantity for each of the 900 grid cells and theory tells us that, by taking a random sample, we can expect to obtain estimators (e.g., of the population mean of all 900 grid cells) with

good statistical properties, where the expectation is over realizations of the sample of 100 grid cells. For example, if we repeatedly draw samples of size 100 then, over many such samples, the expected value of the estimator may be unbiased. Conversely, in the SCR modeling framework, properties of our estimators are distinctly model based. We evaluate estimators (usually) or care only about a *fixed* sample of spatial locations, averaged over realizations of the underlying process and data we might generate. Although sometimes we might condition on the data for purposes of inference (if we have our Bayesian hat on), the probability model for the data is fundamental to inference, and the spatial sample of trap locations is always fixed. It therefore makes sense to seek a trap configuration that we expect to produce precise estimates of SCR model parameters, and not judge our design by averaging over many randomly (or otherwise chosen) trap configurations.

10.1.2 Sampling space or sampling individuals?

A fundamental question in any sampling problem is what is the sample frame—or the population we are hoping to extrapolate our sample to. In the context of capture-recapture studies, it is tempting to think of the sample frame as being spatial (the space within “the study area,” tiled into quadrats perhaps). Clearly SCR models involve a type of spatial sampling—we have to identify spatial locations for traps, or arrays of traps. However, unlike conventional natural resource sampling the attribute we measure is *not* directly relevant to the *sample location*, such as where we place a trap and, therefore, it may not be sensible to think of the sample frame as being comprised of spatial units. On the other hand, capture-recapture studies clearly obtain a sample of *individuals* and SCR models are models of *individual* encounter and space use. Therefore, it is more natural to think of the sample frame as a list of N individuals, determined by the definition of the state-space, or a subset of the state-space, i.e., the study area, but the number N is unknown. The purpose of the SCR study is to draw a sample of these N individuals and learn about an individual attribute—namely, where that individual lives. *That* is the sampling context of SCR models. SCR models link the observed data (encounter histories) to this individual attribute via a model (with parameters) which we need to fit. Once we fit that model, we usually use it to make a prediction or estimate the attribute for individuals that did not appear in the sample.

Spatial sampling in SCR studies is important, but only as a device for accumulating individuals in the sample from which we can learn about their inclusion probability. That is, we’re not interested in any sample unit attribute directly but, rather, we use spatial units as a means for sampling individuals and obtaining individual-level encounter histories. It makes sense in this context that we should want to choose a set of spatial sample units that provides an adequate sample size of individuals, perhaps as many as possible. The key technical consideration as it relates to spatial sampling and SCR, is that arbitrary selection of sample units has a side-effect that it induces unequal probabilities of inclusion of the sample units (i.e., an individual exposed to more traps is more likely to be included into the sample than an individual exposed to few traps) and so we must also learn about these unequal probabilities of sample inclusion.

The fact that SCR sampling induces unequal probabilities of sampling is consistent with the classical sampling idea of Horvitz-Thompson estimation which has motivated capture-recapture models similar to SCR (Huggins, 1989; Alho, 1990). In the Horvitz-Thompson framework, the sample inclusion probabilities are usually fixed and known. However, in all real animal sampling problems they are unknown because we never know precisely where each individual lives and therefore cannot characterize its encounter probability. Therefore, we have to estimate the sample inclusion probabilities using a model. SCR models achieve this effect formally, using a fully model-based approach based on a model that accounts for the organization of individual activity centers and trap locations. This notion of Horvitz-Thompson estimation suggests that perhaps we should consider designing SCR studies based on the Horvitz-Thompson variance estimator as a design criterion. We discuss this a little bit later in this chapter.

10.1.3 Focal population vs. state-space

In SCR models we make a distinction between the focal population—the population of individuals we care about—and those of the state-space, which we are required to prescribe in order to fit SCR models. These are not the same thing. The geographic scope of the population of inference is the region within which animals live that you care about in your study—let’s call this “the study area.” This is often prescribed for political reasons or legal reasons (e.g., a National Park). To initiate a study, or perhaps motivating the study, you have to draw a line on a map to delineate a study area, although often it is difficult to draw this line, and where you draw it is not so much a statistical/SCR issue. On the other hand, you need to prescribe the state-space to define and fit an SCR model. This is the region that contains individuals that you *might* capture. This is different from the study area in most cases. To design a study, you need a well-defined study area, but the state-space will also be relevant to efficient distribution of traps, and other considerations.

It is helpful to think about this distinction operationally. We define our study area *a priori*. As a conceptual device, we might think of this as the area that, given an infinite amount of resources, we might wall off so that we can study a real closed population. This “study area” should exist independent of any model or estimator of some population quantity, i.e., the subject-matter context should determine what the study area is. Given a well-defined study area, we use some method to arrange data collecting devices within this study area. The method of arrangement can be completely arbitrary but, naturally, we want to choose arrangements of traps that are better in terms of obtaining statistical information from the data we end up collecting.

Lets face it—it’s quite a nuisance that animals move around and this makes the idea of a spatial study area kind of meaningless in terms of management in most cases. Wherever you draw a line on a map, there will be animals who live mostly beyond that line that will sometimes be subjected to observation in your study. One of the benefits of SCR models is they formalize the exposure and contribution of these individuals to your study. That is a good thing. Thus, you can probably be a bit imprecise or practical in your definition of “the study area” and not worry too much.

With these general concepts of spatial sampling and the sampling of individuals in mind, we can now turn our attention to more specific aspects of study design in SCR surveys, namely the spatial arrangement of detectors. We discuss some general concepts, and then focus on a couple of specific case studies that apply to the Bernoulli observation model or passive detection devices. The general concepts are surely relevant to other SCR models, and we suspect that the specific case studies are relevant as well.

10.2 Study design for (spatial) capture-recapture

The importance of adequate trap spacing and overall configuration of the trapping array has long been discussed in the capture-recapture literature. A heuristic based on recognizing the importance of typical home range sizes (Dice, 1938, 1941) and the need to obtain information about home range size from the trap array is that traps should be spaced such that the array of available traps exposes as many individuals as possible but, at the same time, individuals should be available for capture in multiple traps. Thus, good designs should generate a high sample size n (i.e., the number of individuals captured) and a large number of spatial recaptures. These two considerations form a trade-off in building designs. On one hand, having a lot of traps very close together should produce the most spatial recaptures but produce very few unique individuals captured (assuming that studies are limited in the total number of sampling devices they can deploy). On the other hand, spreading the traps out as much as possible, in a nearly systematic or regular design, should yield the most unique individuals, but probably few spatial recaptures. We will formalize this trade-off later, when we consider formal model-based design of SCR studies.

Traditional CR models require that all individuals in the study area have a probability >0 of being captured, which means that the trap array must not contain “holes” large enough to contain an animal’s entire home range (Otis et al., 1978). The reason why “holes” cause a problem in non-spatial models is that they induce heterogeneity in capture probability. If an animal’s home range lies completely or partially in a hole, then it will have a different probability of being captured than an individual whose home range is peppered with traps. As a consequence, trap spacing is recommended to be on the same order as the radius of a typical home range (e.g., Dillon and Kelly (2007)). For example, imagine a camera trap study implemented in South America with the objective to survey populations of both jaguars (*Panthera onca*) and ocelots (*Leopardus pardalis*). Ocelots have much smaller home ranges and therefore require closer trap spacing than the large, wide-ranging jaguars. The “no holes” assumption entails some strong restrictions with respect to study design. Although we need not cover an area systematically with traps, there has to be some consistent coverage of the entire area of interest. Often, this is achieved by dividing the study area into grid cells, the size of which approximates an average home range (or possibly the smallest home range recorded for the study species in the study area or a similar area; e.g., Wallace et al. (2003)), and then place (at least) one trap within each cell. In many field situations, especially when dealing with large mammals and accordingly large study areas,

achieving this consistent coverage can be extremely challenging or even impossible. Depending on local environmental conditions, parts of the study area can be virtually inaccessible to humans, because of dense vegetation cover, or unsuitable for setting up detectors, because of flooding. Even when accessible, setting up traps in difficult habitat conditions can consume disproportional amounts of time, manpower, and other resources. Regardless of whether the trap spacing does result in holes or not, the problem of spatial heterogeneity in capture probability will still exist because individuals with home ranges near the borders of the trap array will have a different probability of being captured than individuals that spend all their time within the trap array.

Where approaches such as mean maximum distance moved (MMDM) are used in combination with traditional CR models to obtain density estimates (see Chapter 4), trap spacing also has a major effect on movement estimates, since it determines the resolution of the information on individual movement (Parmenter et al., 2003; Wilson and Anderson, 1985a). If trap spacing is too wide, there is little or no information on animal movement because most animals will only be captured at one trap (Dillon and Kelly, 2007). In addition, only a trapping grid that is large relative to individual movement can capture the full extent of such movements, and researchers have suggested that the grid size should be at least four times that of individual home ranges to avoid positive bias in estimates of density (Bondrup-Nielsen, 1983). This recommendation originated in small mammal trapping, and it should be relatively easy to follow when dealing with species covering home ranges <1 ha. However, translated to large mammal research, this can entail having to cover several thousands of square kilometers—a logistical and financial challenge that few projects could realistically tackle.

Though closely related, the requirements in terms of spatial study design for SCR models differ distinctly from those for traditional CR. For one, holes in the study area are of no concern in SCR studies. As a practical matter, some animals within the study area might have a vanishingly small probability of being included in the sample, i.e., $p \approx 0$. The nice thing about SCR models is that N is explicitly tied to the state-space, and not the traps that expose animals to encounter. Within an SCR model, extending inference from the sample to individuals that live in these holes represents an extrapolation (prediction of the model outside the range of the data), but one that the model is capable of producing because we have explicit declarations in the model that it applies to any area within the state-space, even to areas where we can't capture individuals because we happened to not put a trap there. Conversely, ordinary capture-recapture models only apply to individuals that have encounter probabilities that are consistent with the model being considered. Presumably, the existence of a hole in the trap array would introduce individuals with $p = 0$, which is not accommodated in those models. This distinction alone allows for completely new and much more flexible study designs in SCR studies, as compared to traditional CR, such as linear designs, "hollow grids" (detectors trace the outline of a square), or small clusters of grid spread out over larger landscapes (Efford et al., 2005, 2009a; Efford and Fewster, 2012).

Whereas traditional CR studies are concerned with the number of individuals and recaptures and with satisfying the model assumption of all individuals having some probability of being captured, in spatial capture-recapture we are looking at

an additional level of information: We need spatially dispersed captures and recaptures. It is not enough to recapture an individual—we need to recapture at least some individuals at several traps. Therefore, in general, design of SCR studies boils down to obtaining three bits of information: total unique individuals captured, total number of recaptures informative about baseline encounter rate, and spatial recaptures, informative about σ .

Most SCR design choices wind up trading these three things against each other to achieve some optimal (or good) mix. So, for example, if we sample each of a very small number of sites a huge number of times then we can get a lot of recaptures but only very few spatial recaptures, and few unique individuals, etc. This need for spatial recaptures may appear as an additional constraint on study design, but actually, SCR studies are much less restricted than traditional CR studies, because of the way animal movement is incorporated into the model: σ is estimated as a specified function of the ancillary spatial information collected in the survey and the capture frequencies at those locations. This function is able to make a prediction across distances even when these are latent, including distances larger than the extent of the trap array. When there is enough data across at least some range of distances, the model will do well at making predictions at unobserved distances. The key here is that there needs to be “enough data across some range of distances,” which induces some constraint on how large our overall trap array must be to provide this range of distances (e.g., [Marques et al., 2011](#); [Efford, 2011b](#)). We will review the flexibility of SCR models in terms of trap spacing and trapping grid size in the following section.

10.3 Trap spacing and array size relative to animal movement

Using a simulation study, [Sollmann et al. \(2012\)](#) investigated how trap spacing and array size relative to animal movement influence SCR parameter estimates, and we will summarize their study here. They simulated encounter histories on an 8×8 trap array with regular spacing of 2 units, using a binomial observation model with a Gaussian hazard encounter model and a baseline detection rate $\lambda_0 = 0.5$ on the cloglog scale, across a range of values for the scale parameter σ^* . We refer to the scale parameter as σ^* here, because [Sollmann et al. \(2012\)](#) use a slightly different parametrization of SCR models, in which σ^* corresponds to $\sigma \times \sqrt{2}$. The trap array was buffered by $3 \times$.

In Section 5.4 we pointed out that under the Gaussian (or half-normal) detection model σ can be converted into an estimate of the 95% home range or “use area” around \mathbf{s}_i . Based on this transformation, values for σ^* were chosen so that there was a scenario where the trap array was smaller than a single individual’s home range, i.e., trap spacing was small relative to individual movements ($\sigma^* = 5$ units), a scenario where spaces between traps were large enough to contain entire home ranges ($\sigma^* = 0.5$ units), and two intermediate scenarios and where σ^* was smaller ($\sigma^* = 1$ unit) and larger ($\sigma^* = 2.5$ units) than the trap spacing, respectively. N was

Table 10.1 Mean, relative root mean squared error (RRMSE) of the mean, mode, 2.5% and 97.5% quantiles, relative bias of mean (RB), and 95% Bayesian credible interval (BCI) coverage for spatial capture-recapture parameters across 100 simulations for four simulation scenarios, defined by the input value of movement parameter σ^* . N = number of individuals in the state-space; λ_0 = baseline trap encounter rate.

Scenario	Mean	RRMSE	Mode	2.5%	97.5%	RB	BCI
$\sigma^* = 1$ ($\sigma = 0.71$)							
N	108.497	0.172	104.099	78.977	143.406	0.085	96
λ_0	0.518	0.248	0.477	0.303	0.752	0.035	94
σ^*	1.008	0.093	0.990	0.857	1.195	0.008	94
$\sigma^* = 2.5$ ($\sigma = 1.77$)							
N	100.267	0.105	98.456	82.086	121.878	0.003	97
λ_0	0.507	0.118	0.500	0.409	0.623	0.014	92
σ^*	2.501	0.046	2.491	2.267	2.690	<0.001	92
$\sigma^* = 5$ ($\sigma = 3.54$)							
N	102.859	0.137	100.756	77.399	130.020	0.029	88
λ_0	0.505	0.075	0.501	0.435	0.580	0.011	93
σ^*	5.023	0.039	5.001	4.687	5.431	0.005	97

100, the baseline trap encounter rate λ_0 was 0.5 (on the cloglog scale) for all four scenarios and trap encounters were generated over four occasions. Table 10.1 shows the results as the average over 100 simulations.

All model parameters were estimated with relatively low bias (<10%) and high to moderate precision (relative root mean squared error, RRMSE < 25%) for all scenarios of σ^* , except $\sigma^* = 0.5$ units, under which model parameters were mostly not estimable (therefore excluded from Table 10.1). Data for the latter case mostly differed from the other scenarios in that fewer animals were captured and very few of the captured animals were recorded at more than 1 trap (Table 10.2). For $\sigma^* = 0.5$, abundance (N) was not estimable in 88% of the simulations, and when estimable, was

Table 10.2 Summary statistics of 100 simulated data sets for four simulation scenarios, defined by the input value of movement parameter σ^* . Individual detection histories were simulated on an 8×8 trap array with regular trap spacing of 2 units.

Scenario	Inds. Captured	Total Captures	Inds. Recaptured	Inds. Captured at >1 Trap
$\sigma^* = 0.5$	18.29 (3.84)	25.38 (5.86)	5.52 (2.03)	0.72 (0.95)
$\sigma^* = 1.0$	37.70 (13.44)	69.35 (26.05)	19.48 (7.68)	11.87 (5.43)
$\sigma^* = 2.5$	44.19 (4.67)	231.78 (33.98)	36.60 (4.76)	35.21 (4.73)
$\sigma^* = 5.0$	40.51 (5.15)	427.77 (79.09)	33.09 (4.63)	32.60 (4.76)

underestimated by approximately 50%. This shows that a wide trap spacing that is considerably too large relative to animal movement may be problematic in SCR studies.

Estimates (posterior means) of N were least biased and most precise under the $\sigma^* = 2.5$ scenario, and in general, all parameters were estimated best under the $\sigma^* = 2.5$ or the $\sigma^* = 5$ scenario. All estimates had the highest relative bias and the lowest precision under the $\sigma^* = 1$ scenario. These results clearly demonstrate that SCR models can successfully handle a range of trap spacing to animal movement ratios, and even perform well when using a trap array smaller than an average home range: at $\sigma^* = 5$, the home range of an individual was approximately 235 units², while the trapping grid only covered 196 units².

An important consideration in this simulation study is that all but the $\sigma^* = 0.5$ units scenarios provided reasonably large amounts of data, including 20+ individuals captured. When dealing with real-life animals, which are often territorial and may have lower trap encounter rates, a very small grid area compared to an individual's home range may result in the capture of very few individuals. In that case, the sparse data will limit the ability of the model to estimate parameters (Marques et al., 2011), which is true of most models.

To further explore the effects of trap spacing and movement on bias and precision of estimates of N , we expanded the simulation study of Sollmann et al. (2012): we considered a regular 7×7 grid, with trap spacing ranging from $0.5 \times \sigma$ to $4 \times \sigma$, with a state-space that had variable size so that the buffer around the traps was constant in units of σ . For each trap spacing scenario we simulated and analyzed 500 data sets and calculated the RRMSE and relative bias for the estimates of N . Figure 10.1 shows the results of this set of simulations. We see that there is clearly an optimal trap spacing, especially in terms of precision, which is highest at a trap spacing of $1.5 - 2.5 \times \sigma$. Efford (2012) reported similar results and highlighted the trade-off between the number of individuals captured and the number of spatial

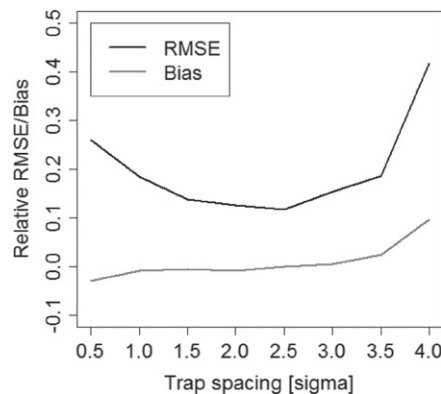


FIGURE 10.1

Relative bias and relative RMSE of estimates of N from an SCR model for a range of trap spacing scenarios.

recaptures—intuitively, the former goes up with an increase in trap spacing, whereas the latter goes down. In summary, in small trap spacing scenarios, the small sample size leads to imprecise estimates, whereas in large trap spacing scenarios, lack of spatial recaptures leads to imprecise and biased estimates.

10.3.1 Black bears from Pictured Rocks National Lakeshore

To see how trap array size influences parameter estimates from spatial capture-recapture models in the real world, [Sollmann et al. \(2012\)](#) also looked at a black bear data set from Pictured Rocks National Lakeshore, Michigan, collected using 123 hair snares distributed over an area of 440 km² along the shore of Lake Superior in May–July 2005 ([Belant et al., 2005](#)). The SCR model for the bear data included sex-specific encounter rate parameters, and an occasion-specific baseline encounter rate. This was motivated by (a) the lower average number of detections for male bears, (b) the decreasing number of detections over time in the raw data, and (c) the fact that male black bears are known to move over larger areas than females (e.g., [Koehler and Pierce, 2003](#); [Gardner et al., 2010b](#)).

To address the impact of a smaller trap array on the parameter estimates, models fitted to the full data set were compared to models fitted to data subsets. The first subset retained only those 50% of the traps closest to the grid center. In the second subset, only the southern 20% of the traps were retained.

Reducing the area of the trap array by 50% created a grid polygon of 144 km², which was smaller than an estimated male black bear home range and only 50% larger than a female black bear home range—approximately 260 km² and 100 km², respectively, when converting estimates of σ^* to home range size. Table 10.3 shows that this did not greatly influence model results, compared to the full data set.

Table 10.3 Posterior summaries of SCR model parameters for black bears, modified from [Sollmann et al. \(2012\)](#).

	Mean (SE)	Mode	2.5%	97.5%
Full data set				
D	10.556 (1.076)	10.448	8.594	12.792
σ^* (males)	7.451 (0.496)	7.323	6.579	8.495
σ^* (females)	2.935 (0.143)	2.939	2.671	3.226
50% of traps				
D	12.648 (1.838)	12.205	9.307	16.713
σ^* (males)	5.354 (0.511)	5.248	4.472	6.473
σ^* (females)	3.318 (0.277)	3.262	2.841	3.910
20% of traps				
D	6.752 (1.611)	5.953	4.000	10.218
σ^* (males)	9.881 (3.572)	7.566	5.121	18.447
σ^* (females)	2.686 (0.391)	2.657	2.121	3.404

Removing 80% of the traps and thereby reducing the area of the trap array to 64 km²—well below the average black bear home range—had a great effect on sample size (only 25 of the original 83 individuals sampled) and parameter estimates. Particularly, male black bear movement was overestimated and imprecise. The combination of a low baseline trap encounter rate of males and the considerable reduction in sample size led to a low level of information on male movement: 5 of the 12 males were captured at one trap only. Although they moved over smaller areas, owing to their higher trap encounter rate, females were, on average, captured at more traps (3.4 traps per individual, compared to 2.6 for males) so that their movement estimate remained relatively accurate. Overestimated male movements and female trap encounter rates resulted in an underestimate of density of almost 40%. This effect is contrary to what we would expect to see in non-spatial CR models, where a trapping grid that is small relative to animal movement leads to underestimated movement (MMDM) and overestimated density (Bondrup-Nielsen, 1983; Dillon and Kelly, 2007; Maffei and Noss, 2008). While this example again demonstrates the ability of SCR models to deal with a range of trapping grid sizes, it also clearly shows that your study design needs to consider the amount of data you can expect to collect. As an alternative to simulation studies, Efford et al. (2009b) provide a mathematical procedure to determine the expected number of individuals captured and recaptures for a given detector array and set of model parameters.

10.4 Sampling over large areas

Trap spacing is an essential aspect of design of SCR studies. However, it is only the most important aspect if one can uniformly cover a study area with traps. In many practical situations, where the study area is large relative to effort that can be expended, one has to consider other strategies that deviate from a strict focus on trap spacing. There are two general strategies that have been suggested for sampling large areas, which we think are useful in practice, either by themselves or combined: Sampling based on *clusters* of traps and sampling based on *rotating* groups of traps over the landscape.

Karanth and Nichols (2002) describe three strategies for moving traps to achieve coverage of a larger study area, geared toward traditional capture-recapture analysis. Suppose that sampling the entire area of interest requires sampling G sites, then the three strategies are:

1. For every day/sampling occasion, randomly choose x out of your G sites, where x is the number of trapping devices you have at hand. Obviously, this requires that it be relatively easy to move traps around.
2. Move blocks of traps daily that are in proximity to one another. For example, if you divide your total study area into four blocks, sample block 1 for a day, then move traps to block 2 for a day, and so forth, and repeat until each block has been sampled for a sufficient amount of time.

3. If moving blocks of traps daily is too challenging logistically, then you can sample each block for a certain number of days/occasions before moving them to the next block. In this fashion, you only need to move traps to each block once.

In traditional CR we collapse data across traps and assume all individuals in the study area have some probability >0 of being detected. For our data that means that, under scenario (2) the first occasion is defined as the time it takes to sample all 4 blocks once, the second occasion consists of the second round of sampling all blocks, etc. Under scenario (3), we have to combine data from day 1 in each of the blocks to form occasion 1, data from day 2 in each of the blocks forms occasion 2, and so on. Especially scenario 3 makes modeling time-dependent detection difficult, since occasion 1 does no longer refer to an actual day or continuous time interval. We do not have that problem in SCR, where accounting for sampling effort at each trap is straightforward, as we first demonstrated for the wolverine example in Section 5.9. Because we are dealing with detection at the trap level, even for design (3) in a spatial framework, we can still look at variation in detection over time. As such, we don't think that one of the above designs is better than the other for SCR models, but rather, all of them may produce adequate SCR data, as long as overall sample size requirements are met.

Efford and Fewster (2012) looked at the performance of different spatial study designs for abundance estimation from traditional and spatial capture-recapture models, including a clustered design, where groups of detectors are spaced throughout the larger region of interest. They found that in a spatial framework this design performed well, although there were indications of a slight positive bias in estimates of N . Such a clustered design enables researchers to increase area coverage without having to increase the number of traps. Efford and Fewster (2012) note that distribution of clusters has to be spatially representative—for example, systematic with a random origin. The issue of spatially representative designs is not limited to SCR and an extensive treatment of the topic can be found in the distance sampling literature (Buckland et al., 2001). Further, the authors stress that, if distances among clusters are large and individuals are unlikely to show up in several clusters, then the method relies on spatial recaptures *within* clusters, meaning that spacing of detectors within clusters has to be appropriate to the movements of the species under study. A clustered type of design is also suggested by Efford et al. (2009b) for acoustic detectors (see Chapter 9.4) with small groups of such detectors (e.g., 2×2) being distributed in a probabilistic fashion across the region of interest.

In practice, employing both of these strategies—clustering and rotating traps—might be necessary or advantageous. Sun (2013) used a simulation study to investigate different trap arrangements (Figure 10.2) for a black bear study based on hair snares distributed over a 2625-km² study area. She simulated detection data of bears for three trap arrangements including a regular (uniform) coverage of traps, clusters of 4 traps each with a gap between clusters, and a design in which the clusters were moved midway through the study to fill the gap (a sequential or “rotating” design). She found that the precision and accuracy of estimates of N generally decreased when changing

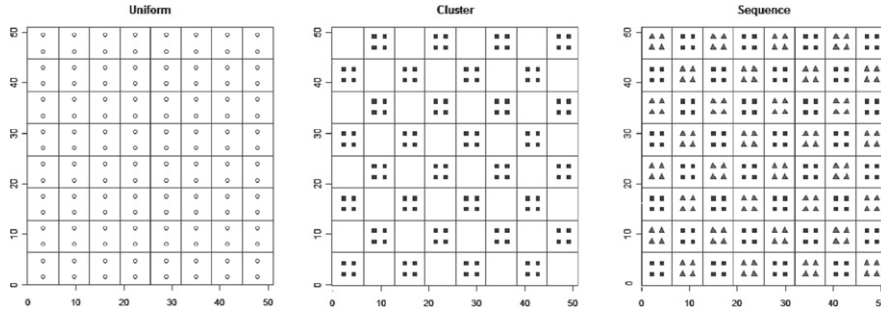


FIGURE 10.2

Three designs evaluated by Sun (2013). The left panel shows uniform coverage of the area with traps (hair snares) equally spaced and static for the duration of the period. The central panel shows clusters of four traps in close proximity, with larger gaps between clusters. The right panel shows a design in which all grid cells are sampled by the cluster of 4 traps, but in a sequential (in time) manner.

from a uniform to a clustered to a rotating design, although the loss of efficiency was relatively small when using the clustered design. The result seems to support that cluster designs can be effective with relatively little loss of efficiency.

Further research on optimal detector configurations, especially for large scale studies, is called for (Efford and Fewster, 2012). More generally, work on formalizing and generalizing these ideas of spatial study design is needed. We believe the model-based spatial design approach that we introduce below is one possible way to tackle that.

10.5 Model-based spatial design

A point we have stressed in previous chapters is that SCR models are basically glorified versions of generalized linear models (GLMs) with a random effect that represents a latent spatial attribute of individuals, the activity center or home range center. This formulation makes analysis of the models readily accessible in freely available software and allows us to adapt and use concepts from this broad class of models to solve problems in spatial capture-recapture. In particular, we can exploit well-established model-based design concepts (Kiefer, 1959; Box and Draper, 1959, 1987; Fedorov, 1972; Sacks et al., 1989; Hardin and Sloane, 1993; Fedorov and Hackl, 1997) to develop a framework for designing spatial trapping arrays for capture-recapture studies. Müller (2007) provides a recent monograph level treatment of the subject that is very accessible.

In the following sections, we adapt these classical methods for constructing optimal designs to obtain the configuration of traps (or sampling devices) in some region (the design space, \mathcal{X}), that minimizes some appropriate objective function based on the variance of model parameters, α , or N , for a prescribed state-space. In particular,

we show that a criterion, based on the variance of an estimator of N , represents a formal compromise between minimizing the variance of the MLEs of the detection model parameters and obtaining a high expected probability of capture. Intuitively, if our only objective was to minimize the variance of parameter estimates then all of our traps should be in one or a small number of clusters where we can recapture a small number of individuals many times each. Conversely, if our objective was only to maximize the expected probability of encounter then the array should be highly uniform so as to maximize the number of individuals being exposed to capture.

10.5.1 Statement of the design problem

Let \mathcal{X} , the *design space*, denote some region within which sampling could occur and let $\mathbf{X} = \mathbf{x}_1, \dots, \mathbf{x}_J$ denote the *design*, the set of sample locations (e.g., of camera traps), normally we just call these “traps.” The design space \mathcal{X} must be prescribed (a priori). Operationally, we could equate \mathcal{X} to the study area itself (which is of management interest) but, in practical cases, there will generally be parts of the study area that we cannot sample. Those areas need to be excluded from \mathcal{X} . While \mathcal{X} may be continuous, in practice it will be sufficient to represent \mathcal{X} by a discrete collection of points which is what we do here. This is especially convenient when the geometry of \mathcal{X} is complicated and irregular, which would be the case in most practical applications. The technical problem addressed subsequently is how to choose the locations \mathbf{X} in a manner that produces the “optimal” (lowest variance) for estimating population size or density, or some other quantity of interest.

As usual, we regard the population of N individual activity centers as the outcome of a point process distributed uniformly over the state-space \mathcal{S} . The relevance and importance of \mathcal{S} has been established repeatedly in this book, as it defines a population of individuals (i.e., activity centers) and, in practice, it is not usually the same as \mathcal{X} due to the fact that animals move freely over the landscape and the location of traps is typically restricted by policies, ownership, logistics, and other considerations. The objective we pursue here is: Given (1) \mathcal{X} , (2) a number of design points, J ; (3) the state-space \mathcal{S} , (4) an SCR model, and (5) a design criterion $Q(\mathbf{X})$, we want to choose *which* J design points we should select in order to obtain the *optimal* design under the chosen model, where the optimality is with respect to $Q(\mathbf{X})$.

What types of functions make reasonable objective functions, $Q(\mathbf{X})$? We will describe some possible choices for $Q(\mathbf{X})$ below, but it makes sense that they should relate to the variance of estimators of one or more parameters of the SCR model.

We motivate the basic ideas of model-based design with a simple model that proves to be an effective caricature of the SCR model that we’ll use shortly. Suppose \mathbf{s} is the activity center of a single individual, and \mathbf{s} is known with certainty. Then, for an array of traps \mathbf{X} we measure a response variable, let’s say the strength of an acoustic signal, that has a normal distribution. So we have this response variable that has a normal linear model of the form:

$$\mathbf{y} = \mathbf{M}(\mathbf{X}, \mathbf{s})' \boldsymbol{\alpha} + \mathbf{e}.$$

Where e is random error with $\text{Var}(e) = \delta^2$. In our notation here, $\mathbf{M}(\mathbf{X}, \mathbf{s})$ is some design matrix where, in the context of SCR models, it has 2 columns (for the basic model): A column of 1s, and then a column of distance from each trap \mathbf{x}_j to the activity center \mathbf{s} . The design matrix is therefore, for a single individual, a matrix of dimension $J \times 2$.

The inference objective here is to estimate the parameters $\boldsymbol{\alpha}$. The variance-covariance matrix of $\hat{\boldsymbol{\alpha}}$ is, suppressing the dependence on \mathbf{X} for notational convenience,

$$\text{Var}(\hat{\boldsymbol{\alpha}}, \mathbf{X}) = \delta^2 (\mathbf{M}(\mathbf{s})' \mathbf{M}(\mathbf{s}))^{-1}.$$

Note that the design points \mathbf{x}_j appear explicitly (in the second column of \mathbf{M}). In considering design for estimation in such models it is natural to choose design points such that the variance of $\hat{\boldsymbol{\alpha}}$ is minimized. Here, $\boldsymbol{\alpha}$ is a vector, and so the “variance” is a matrix (at least 2×2) so we have to work with suitable scalar summaries of that matrix, such as the trace (sum of the diagonals) or the determinant, etc.

For a population of N individuals, if we know *all* N values of \mathbf{s} , the design matrix \mathbf{M} has the same basic structure but with N versions stacked up on top of one another, producing a larger $N \times J \times 2$ design matrix. The second column of \mathbf{M} contains the information about trap locations (the first column is still just a column of 1s). Therefore, we could, in principle, find the design \mathbf{X} that optimizes some function of the variance-covariance matrix of the model parameters.

The preceding argument assumes we know the activity centers for each individual in the population. When \mathbf{s} is unknown, it might make sense to consider minimizing the expected (spatially averaged) variance:

$$E_s \{ \text{Var}(\hat{\boldsymbol{\alpha}}, \mathbf{X}) \} = \frac{\delta^2}{nG} \sum_{s \in \mathcal{S}} (\mathbf{M}'(\mathbf{s}) \mathbf{M}(\mathbf{s}))^{-1}.$$

Where nG is the number of points in the discrete representation of the state-space \mathcal{S} . However, this is not the expected variance based on sampling a population of N individuals, just for a single individual having unknown \mathbf{s} . Because of the matrix inverse in this expression, it is not sufficient to use a variance criterion that weights this variance by N . As an alternative, we can maximize the expected *information*, the inverse of the variance-covariance matrix, which is probably more appealing from an analytic point of view. The information matrix for the data based on a single individual, with known \mathbf{s} , is: $\mathcal{I}(\hat{\boldsymbol{\alpha}}, \mathbf{X}) = (\mathbf{M}'(\mathbf{s}) \mathbf{M}(\mathbf{s}))$. For a population of N individuals, let \mathbf{M}_i be the design matrix for the individual with activity center \mathbf{s}_i . Then, the total information for all N individuals is:

$$\mathcal{I}(\hat{\boldsymbol{\alpha}}, \mathbf{X}) = \frac{\delta^2}{nG} \sum_{i=1}^N (\mathbf{M}_i'(\mathbf{s}_i) \mathbf{M}_i(\mathbf{s}_i)).$$

The information matrix depends on the design \mathbf{X} through the N individual matrices $\mathbf{M}_1, \dots, \mathbf{M}_N$. Now, because we don't know each \mathbf{s}_i we must compute the expected total information, over all possible values of \mathbf{s}_i , and for *each* of the N \mathbf{s}_i in the

population, which is an N -fold summation:

$$E_{\mathbf{s}_1, \dots, \mathbf{s}_N} \mathcal{I}(\hat{\boldsymbol{\alpha}}, \mathbf{X}) = \frac{\delta^2}{nG} \sum_{i=1}^N \sum_{\mathbf{s} \in \mathcal{S}} (\mathbf{M}'_i(\mathbf{s}_i) \mathbf{M}_i(\mathbf{s}_i)),$$

which is just N copies of the expected (spatially averaged) information:

$$E_{\mathbf{s}_1, \dots, \mathbf{s}_N} \mathcal{I}(\hat{\boldsymbol{\alpha}}, \mathbf{X}) = \frac{N\delta^2}{nG} \sum_{\mathbf{s} \in \mathcal{S}} (\mathbf{M}'_i(\mathbf{s}_i) \mathbf{M}_i(\mathbf{s}_i)).$$

It therefore seems sensible to base design of SCR studies on some criterion that is a function of this expected information matrix, e.g., find the design that maximizes the diagonals, or the determinant, or minimizes the trace of the *inverse* (the variance-covariance matrix based on N individuals). This can be done for any number of design points $\mathbf{x}_1, \dots, \mathbf{x}_J$ using standard exchange algorithms (see Müller, 2007, Chapter 3) and we discuss this below in Section 10.5.5. However, our SCR models are not normal linear models but, rather, more like Poisson or binomial GLMs. We see in the next section that we can adapt these ideas for such models.

10.5.2 Model-based Design for SCR

Following our development of the normal linear model above, suppose for the moment that we know \mathbf{s} for a single individual. In this case, its vector of encounter frequencies in each trap \mathbf{y} are either binomial or Poisson counts, and the linear predictor has this form:

$$g(\mathbb{E}(\mathbf{y})) = \alpha_0 + \alpha_1 d(\mathbf{x}, \mathbf{s})^2, \quad (10.5.1)$$

for the Gaussian encounter probability model, and where $d(\mathbf{x}, \mathbf{s})$ is the distance between trap location \mathbf{x} and individual activity center \mathbf{s} . In vector form, we write this as:

$$g(\mathbb{E}(\mathbf{y})) = \mathbf{M}'\boldsymbol{\alpha},$$

where \mathbf{M} is the $J \times 2$ design matrix where the second column contains the squared pairwise distances between the activity center for individual i and trap j , and thus it depends on both \mathbf{X} and \mathbf{s} .

The asymptotic formula for $\text{Var}(\boldsymbol{\alpha})$ can be cooked up for any type of GLM. As an example (we make use of this in Section 10.5.1), for the Poisson GLM, the asymptotic variance-covariance matrix of $\hat{\boldsymbol{\alpha}}$, considering a single individual having location \mathbf{s} , is¹

$$\text{Var}(\hat{\boldsymbol{\alpha}}|\mathbf{X}, \mathbf{s}) = (\mathbf{M}(\mathbf{s})'\mathbf{D}(\boldsymbol{\alpha}, \mathbf{s})\mathbf{M}(\mathbf{s}))^{-1}. \quad (10.5.2)$$

This is a function of the design \mathbf{X} as well as \mathbf{s} , both of which are balled up in the regression design matrix \mathbf{M} , and the matrix \mathbf{D} which is a diagonal matrix having

¹This is basic GLM theory that derives from the fact that the Poisson is a member of the natural exponential family of distributions, e.g., see McCullagh and Nelder (1989) or Agresti (2002).

elements $\text{Var}(y_j|\mathbf{s}) = \exp(\mathbf{m}'\boldsymbol{\alpha})$ for y_j = the frequency of encounter in trap j and where \mathbf{m}' is the j th row of $\mathbf{M}(\mathbf{s})$. We can compute the expected information under the Poisson model with known N , as in Section 10.5.1, using this modified formulation.

These ideas are meant to motivate technical concepts related to model-based design, where we know N , and therefore have a convenient variance or information expression to work with. However, in all real capture-recapture applications we won't know N , and so we need to address that issue, which we do in the next section.

10.5.3 An optimal design criterion for SCR

There are a number of appealing directions to pursue for deriving a variance-based criterion upon which to devise designs for spatial capture recapture studies. For one, we could formulate the objective function based on the variance of the Huggins-Alho estimator (Section 4.5) of N . We find that these expressions depend on individual sample inclusion probabilities (if \mathbf{s} is close to traps, the individual has a high probability of being encountered and *vice versa*), and hence the specific trap locations, and parameters of the model. These variance expressions provide a natural design criterion. As an alternative, we devise a variance criterion based on the conditional estimator of N having the form

$$\hat{N}_c = \frac{n}{\hat{\bar{p}}},$$

where $\hat{\bar{p}}$ is the MLE of the marginal probability that an individual appears in the sample of n unique individuals, and it depends on the MLE of the parameters of the encounter probability model, $\hat{\boldsymbol{\alpha}}$. We elaborate on the precise form of $\hat{\bar{p}}$ and the variance of its MLE below. The variance of this estimator is:

$$\text{Var}\left(\frac{n}{\hat{\bar{p}}}\right) = n^2 \times \text{Var}\left(\frac{1}{\hat{\bar{p}}}\right).$$

An important thing to note is that this estimator, and its variance, are *conditional* on the sample size of individuals, n . To “uncondition” on n . Fortunately, this is a simple proposition using, we use standard rules of expectation and variance, which produces the following expression:

$$\text{Var}(\hat{N}_c(\boldsymbol{\alpha})) = N\bar{p} \{(1 - \bar{p}) + N\bar{p}\} \left(\frac{\text{Var}(\hat{\bar{p}})}{\bar{p}^4} \right). \quad (10.5.3)$$

This expression provides an intuitively appealing criterion upon which to devise SCR designs for two reasons: (1) It depends on \bar{p} , the marginal probability of encounter. Clearly the variance decreases as \bar{p} increases and, therefore, as the expected sample size of individuals increases, we will obtain a more precise estimate of N . In general, the form of \bar{p} depends on the SCR model being used. We will provide an example below. Obviously, \bar{p} will also depend on the parameter values $\boldsymbol{\alpha}$. (2) The criterion depends on $\text{Var}(\hat{\bar{p}})$. So, designs that estimate \bar{p} well should be preferred. This will also depend on the parameters $\boldsymbol{\alpha}$ and *also* the variance of the MLE, $\hat{\boldsymbol{\alpha}}$. Based on these

considerations, we suggest a number of criteria for constructing spatial designs for capture-recapture studies. For convenience we label them $Q_1 - Q_4$:

1. $Q_1 = \text{Trace}(\mathbf{V}_{\hat{\alpha}})$ where $\mathbf{V}_{\hat{\alpha}}$ is the variance-covariance matrix of the MLE of α . Designs which minimize this criterion are those which are good for estimating the parameters of the encounter probability model.
2. Q_2 is the variance expression in Eq. (10.5.3). Using this criterion, we should prefer designs that minimize the variance for estimating N .
3. $Q_3 = 1 - \bar{p}$. Designs which minimize this criterion are those which maximize the average capture probability. These should maximize the expected sample size, n .
4. $Q_4 = \text{Var}(\hat{\bar{p}})$. Designs that minimize this criterion provide good estimates of \bar{p} .

An important thing to observe is that all of these criteria are functions of the true population size, N , and/or the true parameter values of the encounter probability model. Therefore, to use these criteria in the context of devising SCR designs, we need to have some idea of their values, or be able to obtain estimates from the literature, or a pilot study. Of course, this is not a typical in the development of sampling designs based on statistical models. However, putting some thought into reasonable values of parameters then gives us a basis for choosing designs that are optimal for our intended estimation objective. We discuss optimizing these or other design criteria over all possible designs in Section 10.5.5.

10.5.4 Too much math for a Sunday afternoon

Here we discuss the calculation of \bar{p} and the variance expressions required to compute the design criteria above, for a particular SCR model.

10.5.4.1 Characterizing \bar{p}

In SCR models, an individual with activity center \mathbf{s}_i is captured if it is captured in *any* trap and therefore, under the Bernoulli (passive detector) observation model,

$$\bar{p}(\mathbf{s}_i, \mathbf{X}) = 1 - \prod_{j=1}^J (1 - p_{ij}(\mathbf{x}_j, \mathbf{s}_i)),$$

where p_{ij} here is the Gaussian (or other) encounter probability model that depends on distance between traps and activity centers. Using the Gaussian hazard model, we have:

$$\bar{p}(\mathbf{s}_i, \mathbf{X}) = 1 - \exp \left(-\lambda_0 \sum_j \exp \left(\alpha_1 \times d(\mathbf{x}_j, \mathbf{s}_i)^2 \right) \right),$$

where $\lambda_0 = \exp(\alpha_0)$. Here we emphasize that this is conditional on \mathbf{s}_i and also the design—the trap locations \mathbf{x}_j . The *marginal* probability of encounter, i.e., averaging

over all possible locations of \mathbf{s} , is:

$$\bar{p}(\mathbf{X}) = 1 - \int_{\mathbf{s}} \bar{p}(\mathbf{s}_i, \mathbf{X}) d\mathbf{s}. \quad (10.5.4)$$

This can be calculated directly *given* the design \mathbf{X} , and parameters of the model. This is handy because it is used in the variance formulae given subsequently and it is needed to evaluate any of the criteria described above.

10.5.4.2 Characterizing $\text{Var}(\hat{p})$

Developing an expression for $\text{Var}(\hat{p})$ depends on the observation model. We work here with the Poisson observation model, and we do that because the technical argument that follows is somewhat easier for that case compared to the Bernoulli model for passive detection devices (but see [Huggins \(1989\)](#) and [Alho \(1990\)](#) for additional context related to computing asymptotic variance expressions under a Bernoulli encounter model). We first express the integral in Eq. (10.5.4) as a summation over a fine mesh of points so that:

$$\bar{p}(\mathbf{X}) = \frac{1}{nG} \sum_{\mathbf{s}} 1 - \bar{p}(\mathbf{s}_i, \mathbf{X}),$$

which, under the Gaussian encounter probability model is:

$$\bar{p}(\mathbf{X}) = \frac{1}{nG} \sum_{\mathbf{s}} \left\{ 1 - \exp \left(- \sum_j \exp \left(\alpha_0 + \alpha_1 d(\mathbf{x}_j, \mathbf{s})^2 \right) \right) \right\}$$

To obtain the MLE of $\bar{p}(\mathbf{X})$ we plug in the MLE of α_0 and α_1 , in this case $\hat{\lambda}_0 = \exp(\hat{\alpha}_0)$ and $\hat{\alpha}_1$. To compute the variance of the MLE of \bar{p} , we note that the variance operator can move inside the summation over \mathbf{s} , and the subtraction from 1 doesn't affect variance, so we have

$$\text{Var}(\hat{p}(\mathbf{X})) = \sum_{\mathbf{s}} \text{Var} \left(\exp \left(- \sum_j \exp \left(\hat{\alpha}_0 + \hat{\alpha}_1 d(\mathbf{x}_j, \mathbf{s})^2 \right) \right) \right).$$

A few applications of the delta method and some arm-waving yield the following expression for the variance of \hat{p} :

$$\text{Var}(\hat{p}(\mathbf{X})) = \sum_{\mathbf{s}} \left(\exp(-\hat{\lambda}_{\mathbf{s}}) \right) \left(\sum_j \hat{\lambda}(\mathbf{x}_j, \mathbf{s})^2 \left(\text{Var}(\hat{\alpha}_0) + d(\mathbf{x}_j, \mathbf{s})^4 \text{Var}(\hat{\alpha}_1) \right) \right),$$

where $\hat{\lambda}(\mathbf{x}, \mathbf{s}) = \exp(\hat{\alpha}_0 + \hat{\alpha}_1 d(\mathbf{x}, \mathbf{s})^2)$ and $\hat{\lambda}_{\mathbf{s}} = \sum_{j=1}^J \hat{\lambda}(\mathbf{x}_j, \mathbf{s})$.

10.5.4.3 Characterizing $\text{Var}(\hat{\alpha})$

For a given design \mathbf{X} , we just showed how to compute $\text{Var}(\hat{p}(\mathbf{X}))$ —this is just a calculation involving sums over all points in the state-space and design points—provided we know the variance of the estimator of α , $\text{Var}(\hat{\alpha})$, and the true values of the parameters of the encounter probability model. However, it is not so easy to write down the analytic form of the matrix $\text{Var}(\hat{\alpha})$. Some calculus would have to be done on the conditional likelihood (e.g., from [Borchers and Efford, 2008](#)) to figure out the asymptotic form of this matrix. For our purposes, we think it might suffice² to approximate the matrix, using the analogous result from a Poisson or binomial GLM assuming that N is known, since we have convenient formulas for those (see Eq. (10.5.2)).

The approximate variance given by Eq. (10.5.2) is conditional on the collection of activity centers, $\mathbf{s}_1, \dots, \mathbf{s}_N$. To resolve this, we take the approach outlined previously (Section 10.5.2) to compute the *expected* information obtained from a particular realization of N individuals, and invert that result.

The expected total (for a population of N individuals) information is N times the expected information:

$$\mathbb{E}(\mathcal{I}(N)) = \frac{N}{nG} \sum_{\mathbf{s}} \mathbf{M}(\mathbf{s})' \mathbf{D}(\mathbf{s}) \mathbf{M}(\mathbf{s}).$$

10.5.4.4 Putting it all together

To make use of these mathematical results to evaluate one of the design criteria, we begin by choosing a design, \mathbf{X} . Given the design, we compute the expected information quantity, invert it to obtain the variance of $\hat{\alpha}$, and then either use that variance matrix in the calculation of criterion Q_1 , or else evaluate some additional quantities along the way to computing the other criteria. We can compute \bar{p} (which is Q_3) for a given design without doing any variance calculations. If we use $\text{Var}(\hat{\alpha})$, along with \bar{p} , we can compute $\text{Var}(\hat{p})$, which is Q_4 . We can combine all of these things together and compute $\text{Var}(\hat{N}_c)$ for a given \mathbf{X} which is Q_2 . This results in values of these various criteria for only a single design that we specified. In practice, we would like to search over the whole “design space” and find the optimal (or at least a very good) design of a given size, J . In the next section, we describe a method for efficiently sorting through the design space.

10.5.5 Optimization of the criterion

To compute spatial designs that optimize a given criterion, we need to prescribe values of the model parameters, or at least come up with a ballpark guess of them so that the criterion can be evaluated for any design, i.e., what are the values of α and N we expect in our study? Once we do that, and specify the state-space, \mathcal{S} , then we can, in theory, optimize any of our variance criteria over all possible configurations of J traps. For small values of J this problem could possibly be solved using standard

²Warning: But we don’t know. No warranty is implied.

numerical optimization algorithms as exist in almost every statistical computation environment. However, J will almost always be large enough so as to preclude effective use of such algorithms. This is a common problem in experimental design, and spatial sampling in general, for which sequential exchange or swapping algorithms have been fairly widely adopted (e.g., Wynn, 1970; Fedorov, 1972; Mitchell, 1974; Meyer and Nachtsheim, 1995; Nychka et al., 1997; Royle and Nychka, 1998). The basic idea is to pose the problem as a sequence of one-dimensional optimization problems in which the objective function is optimized over 1 or several coordinates at a time. In the present case, we consider swapping out \mathbf{x}_j for some point in the design space, \mathcal{X} , that is nearby \mathbf{x}_j (e.g., a first-order neighbor). Beginning with an initial design, chosen randomly or by some other method, the objective function is evaluated for all possible swaps (4 in the case of first-order neighbors) and whichever point yields the biggest improvement in the criterion under consideration is swapped for the current design point. The algorithm is iterated over all J design points and this continues until convergence is achieved. Such algorithms may yield local optima and optimization for a number of random initial designs can yield incremental improvements. We implemented such a swapping algorithm in **R**, and it is available in the `scrbook` package with the function `SCRdesign`. The algorithm operates on a discrete representation of \mathcal{S} (an arbitrary matrix of coordinates). For each point in the design, \mathbf{X} , only the nearest neighbors (the number is specified by the user) are considered for swapping into the design during each iteration. For example, to compute `ndesigns = 10` putative optimal designs (each based on a random start) of size $J = 11$, we execute the function as follows:

```
> des <- SCRdesign(S,X,ntraps=11,ndesigns=10,nn=15,sigma=1)
```

where the state-space \mathcal{S} , and the candidate set \mathcal{X} are provided as matrices, `nn` is the number of nearest neighbors to inspect for each design point change, and `sigma` is the scale parameter of, in this case, a Gaussian hazard model. See the help file `SCRdesign` for examples and analysis of the output.

While swapping algorithms are convenient to implement, and efficient at reducing the criterion in very high-dimensional problems, they do not always yield the global optimum. In practice, as in the examples below, it is advisable to apply the algorithm to a large number of random starting designs. Our experience is that essentially meaningless improvements are realized after searching through a small number of random starts.

The design criteria we developed above bear a striking resemblance to design criteria used to construct so-called space-filling designs (Nychka et al., 1997). Such criteria are based on interpoint distances, and space-filling designs seek to optimize some function of distance alone, instead of a variance-based objective function. The benefit of this approach is that one doesn't have to specify the model to produce a design, and space-filling designs have been shown to provide reasonable approximations to designs based on variance criteria under flexible statistical models (Nychka et al., 1997). An interesting fact about model-based SCR design, is that the criteria

we have outlined above *are* functions of distance alone. This suggests that perhaps other distance-based design criteria might be suitable for SCR models.

10.5.6 Illustration

Because the algorithm operates on a discrete version of \mathcal{S} , it is trivial to apply to situations in which the state-space is arbitrary in extent and geometry. However, we consider a simplified situation here in order to illustrate the calculation of optimal designs and how they look for an idealized situation.

Consider designing a camera trapping study for a square state-space on $[9, 21] \times [9, 21]$ and with \mathcal{X} being the smaller square $[10, 20] \times [10, 20]$. For this illustration we assumed $\alpha_0 = \log(\lambda_0) = -1.7$ and $\sigma = \sqrt{2}$ so that $\alpha_1 = 1/(2\sigma^2) = 1/4$.

Designs of sizes 11 and 21 were computed using 10 random starting designs. We found the optimal design using each of the four criteria we described above. To refresh your memory Q_1 is the trace of the variance-covariance matrix of $\hat{\alpha}$, Q_2 is the variance of \tilde{N} , Q_3 is $1 - \bar{p}$ (so the design that minimizes this criterion obtains the highest possible \bar{p}), and Q_4 is the variance of \hat{p} . The putative optimal designs (henceforth “best”) are shown in Figure 10.3.

The designs are not completely regular but obviously have a systematic look to them. For the $J = 11$ designs, the Q_1 design is slightly more compact, with an average closest neighbor distance of 2.59 units vs 3.03 units for the Q_3 design. The two designs are qualitatively similar, providing roughly uniform coverage of the design space \mathcal{X} . Conversely, the other two criteria produce designs that are highly clustered. Criterion Q_2 , which is optimal for \tilde{N}_c , produces 2 clusters of traps, 7 traps in one and 4 traps in the other. Finally, designs which are optimal for the criterion Q_4 , the variance of estimating \bar{p} , produce a single cluster of traps that is roughly centrally located in the design space. This makes sense, because the very dense cluster of traps provides a large number of recaptures near the origin $d = 0$, which, intuitively, provides the

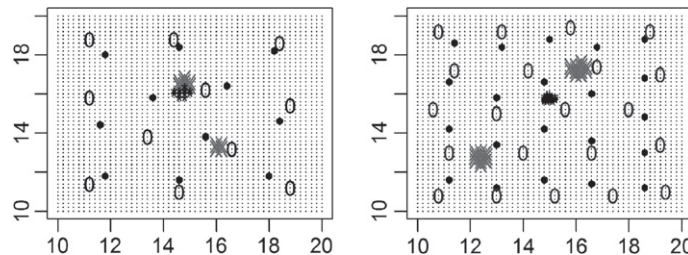


FIGURE 10.3

Best designs for each of 4 design criteria, produced using the exchange algorithm with 15 nearest neighbors and based on 10 random starting designs. The left panel shows the best $J = 11$ designs, and the right panel shows the best $J = 21$ designs. The solid black dots correspond to the best design for Q_1 ; 0 marks the design for Q_3 , tight clusters of “X” for Q_2 and the tightly clustered “*” corresponds to Q_4 .

most information about estimating parameter of the encounter probability model. For the $J = 21$ designs, we have an average closest neighbor distance of 1.87 for Q_1 and 2.19 for Q_3 but, qualitatively, the structure of the designs is similar to $J = 11$. The best design for estimating N (minimizing the criterion Q_2) produces 2 clusters, but just with more traps. While these illustrations make sense to us, we're not entirely convinced of the implication that 2 clusters of traps should be optimal with $J = 21$ total traps. However, it is clear what is going on here is that the tight clusters are providing good information about estimating \bar{p} and, by spreading the two clusters out, the expected sample size, n , is maximized.

While the designs for Q_1 and Q_3 are not exactly uniform, they appear very regular, which we should expect given the regularity of both \mathcal{S} and \mathcal{X} in this case. One thing to note is that the trap spacing varies depending on J *even though* σ is the same, so optimal trap spacing should not be viewed as a static thing depending only on the model. Because the designs are not precisely regular, the average closest neighbor distance is not exactly the same as the trap spacing of a regular grid design.

10.5.7 Density covariate models

Many capture-recapture studies will involve one or more landscape or habitat covariates that are thought to affect density, with the idea of using the methods described in Chapter 11 for modeling and inference. We imagine that it should be possible to extend the model-based framework described previously to accommodate uncertainty due to having to estimate the parameters of the model for density, β , and this could be included as a feature of the design criterion. In this case, we can think of the captures in a trap being Poisson random variables with mean $\mu(\mathbf{x}, \mathbf{s}) \times D(\mathbf{s})$ and the same arguments as given above can be used to devise design criteria and optimize them. However, in this case we might not only care about estimating N but also (or instead) inference about the parameters β . Thus, we might choose designs that are good for N or perhaps only good for estimating β or perhaps both. Intuitively, we think these two design objectives conflict with one another to some extent. Model-based approaches should favor areas of higher density, for estimating N efficiently, but the design must realize variation in the landscape covariates too (T. A. Graves et al., in prep.).

10.6 Temporal aspects of study design

The spatial configuration of traps is one of the most important aspects of sampling design for capture-recapture studies. Indeed, as we discussed in the previous section, design under SCR models can be thought of as being analogous to classical model-based spatial design, and the concepts and methods from that field can be brought to bear on the design of capture-recapture studies. However, there are other aspects of sampling design that should be considered in capture-recapture studies, including the frequency or length of temporal samples. We touch upon some of these issues here, although without a detailed or formal analysis.

10.6.1 Total sampling duration and population closure

All the models we have discussed so far are *closed population* SCR models, i.e., models that assume that the population under study remains constant during our survey. Traditionally, two different levels of closure have been considered in the capture-recapture literature—demographic and geographic closure (see also Chapter 4). Demographic closure refers to the absence of births and deaths, while geographic closure refers to the absence of immigration and emigration during a study. In traditional capture-recapture, the geographic closure assumption prohibited (in theory, not in field praxis, of course) any movement off the trapping grid. [Kendall \(1999\)](#) explored a range of scenarios of closure violation, focusing on different kinds of movement in and out of the study area, and found that several of these scenarios caused biased abundance estimates from traditional capture-recapture models.

As discussed in Chapter 5, one main objective of SCR models is to relax the geographic closure assumption—the model explicitly allows for movements of individuals about their activity centers, which may have them off the trapping grid for parts of the time, even if the activity center itself is on the grid. SCR models do, however, assume no permanent emigration from or immigration into the state-space. The interpretation of demographic closure remains the same in SCR models as it is in traditional CR models.

We have not explored effects of closure violation on SCR abundance and density estimates. Conceptually, we expect estimates to be biased high when births or immigrations happen during our study. For one, the total number of individuals at the study site during the course of the study would be higher than at any particular point in time and correspond to a *cumulative* number of individuals in our study area during the study period. Further, because some individuals are not available for detection for the entire study (they only become available when they are recruited into the state-space) we would expect baseline detection to be underestimated, potentially leading to further positive bias in estimates of abundance. Death or emigrations during a study do not inflate the number of individuals in the state-space, but as animals die and become unavailable for detection, we can again imagine a negative bias in baseline detection and, consequently, some positive bias in N .

To avoid such bias in population estimates, closed population models should typically be applied to short surveys, where short is relative to the life history of the species under study. For example, for small mammals, that might mean a few days, whereas for large, long-lived species with a slow population turnover, several weeks or even a few months can still be considered short enough. In practice, we have no means of guaranteeing a closed population—even if we sample animals for a day, one of the individuals we record may be eaten by a predator later that day, or a dispersing individual may arrive just as we turn our backs. On the other hand, we are faced with the need to collect sufficient data, which, especially for elusive species, pushes us to sample over longer rather than shorter time periods. If we do not have enough sampling devices to cover the entire area of interest at once, rotating study designs (see Section 10.4) can require even longer sampling to accumulate sufficient captures

and recaptures. So clearly, in temporal study design we have to strive for a compromise between collecting enough data while still approximating a closed population. For some species we may be able to avoid seasons where violation of demographic closure is particularly likely—for example, migration seasons in migratory birds, or specific breeding seasons (or collective suicide season in lemmings). But for many species such biological seasons might be less clear cut. For example, in warm climates tigers and other large cats can breed year round (Nowak, 1999). As a consequence, guidelines as to what time frame adequately approximates a closed population are generally vague and arm-wavy. Unfortunately, we do not have much more to offer on the subject of how to decide on the length of a study, other than that to urge you to think about the biology of your study species *before the study* and choose a time window that seems appropriate for that purpose.

10.6.2 Diagnosing and dealing with lack of closure

Once a field study has been conducted, you may wonder whether the collected data contain any evidence that the closure assumption has been satisfied. Relatively few tests for population closure in traditional capture-recapture have been developed, mostly due to the fact that in the data behavioral variation in detection is indistinguishable from violation of demographic closure (Otis et al., 1978; White et al., 1982). Otis et al., (1978) developed a test for population closure that can handle heterogeneity in detection probability, but does not perform well in the presence of time or behavioral variation in p . Stanley and Burnham (1999) developed a closure test for model M_t (time variation in detection), which works well when there is permanent emigration and a large number of individuals migrate. Both tests are implemented in the program **CloseTest** (Stanley and Richards, 2013).

There are no specific population closure tests for SCR models, for the same reasons that violation of other model assumptions cannot necessarily be distinguished from a lack of population closure. If you are worried that closure might have been violated in your study, one approach of dealing with this problem is to fit an open population model. You can subdivide your study into several periods and fit a spatial version of Pollock's robust design capture-recapture model, which can estimate population size/density for each of these periods (in this context also called primary periods) using models of demographic closure. Alternatively, we may consider fully dynamic models, which contain explicit parameters of survival and recruitment (Chapter 16). These models can be quite computationally expensive, and if you wanted a faster, partial check you could alternatively fit a spatial Cormack-Jolly-Seber model, which only estimates survival. The magnitude of the survival estimates gives you some partial information about population closure in your study—if survival is close to 1 there is little evidence of losses of individuals, either through permanent emigration or death. These and other open population models are presented in detail in Chapter 16. Finally, if your data are too sparse to fit a full-blown open population model, you can subdivide your study into $t = 1, 2, \dots, T$ primary periods and estimate abundance separately for each period's worth of data, possibly sharing the detection parameters

across periods, if you can safely assume they remain constant. You can do that by either letting N_i be independent from each other, or by specifying an underlying distribution for all N_i in a multi-session framework as described in Chapter 14.

10.7 Summary and outlook

Design of capture-recapture studies in the context of *spatial* models is an important problem, but solutions to this problem are mostly *ad hoc* or incomplete at the present time. As a general rule, we always recommend scenario analysis by Monte Carlo simulation (Efford and Fewster, 2012; Sollmann et al., 2012; Sun, 2013). This takes a lot of time but it guarantees forward progress, or at least not choosing the dumbest from among several design options. We discussed some examples from the literature that assess trap spacing and evaluate trap clustering and rotating coverage strategies for sampling large areas. The nice thing about simulation studies is that we can generate data for any complex situation we desire, even if we can't fit the model effectively. Thus, we can always characterize worst-case situations under pathological model misspecifications and understand the implications such departures have for parameters estimation.

When designing a spatial capture-recapture study for a single species, trap spacing and the size of the array can (and should) be tailored to the spatial behavior of that species to ensure adequate data collection. However, some trapping devices like camera traps may collect data on more than one species and researchers may want to analyze these data, too. The flexibility in study design of SCR models makes such multi-species approaches more feasible. Independent of the trapping device used, study design will in most cases face a limit in terms of the number of traps available or logistically manageable. As a consequence, researchers need to find the best compromise between trap spacing and the overall grid area.

Particularly for large mammal research, SCR models have much more realistic requirements in terms of area coverage than non-spatial CR models. In the latter, density estimates can be largely inflated with small trapping grids relative to individual movement (Maffei and Noss, 2008)—covering at least four times the average home range is recommended. Further, we need consistent coverage of the entire study area, as all individuals in the population of interest must have some probability >0 to be captured. In contrast, SCR models work well in study areas that are similar in size to an individual's home range (as long as sufficient data is collected) (Sollmann et al., 2012; Marques et al., 2011), and they provide unbiased estimates for sampling designs that do not expose all individuals in the sampled population to detectors, i.e., that have “holes” (Efford and Fewster, 2012). These results, however, should not encourage researchers to design non-invasive trap arrays based on minimum area requirements and with a minimum number of detectors. Study design should still strive to expose as many individuals as possible to sampling and obtain adequate data on individual movement. Large amounts of data, both individuals and recaptures, do not only improve precision of parameter estimates (Sollmann et al., 2012; Efford et al., 2004),

they also allow including potentially important covariates (such as sex or time effects in the black bear example—see also Chapter 7) into SCR models.

Beyond the traditional grid-based sampling design, the flexibility of SCR models allows for different spatial detector arrangements such as dispersed clusters of detectors. How well these different designs perform, comparatively, remains to be explored.

An alternative to simulation-based scenario analysis for constructing spatial designs is a formal model-based strategy in which we seek the configuration of design points (trap locations) $\mathbf{x}_1, \dots, \mathbf{x}_J$ that is optimal for some formal information-based objective function. This is a standard approach in classical sampling and experimentation, yet it has not gained widespread use in ecology. In our view, model-based design under SCR models has great potential due to its coherent formulation and flexibility. On this topic, we have just barely scratched the surface here, showing how to formulate a criterion that is a function of the design, and then optimizing the criterion over all possible designs. Our cursory analysis of model-based design in a single situation did reveal an important aspect of design that has not been discussed in the literature. That is, the optimal spacing of traps in an array depends on the *density* of traps in the state-space. In our analysis, the spacing of 11 and 21 trap optimal designs was quite different. Therefore, this should be considered in practical SCR design exercises.

Conceptually, the information in SCR studies comes in two parts: Recaptures of individuals at different traps (spatial recaptures) and the total sample size of individuals. Maximizing both of these things as objectives induces an explicit trade-off in the construction of capture-recapture designs. We need designs that are good for estimating \bar{p} and also designs that obtain a high sample size of n . Designs that are extremely good only for one or the other will produce bad SCR designs—estimators of density with low precision—or designs in which N is not estimable due to a lack of spatial recaptures. One possible exception is when telemetry data (or other auxiliary data) are available. In Chapter 13 we discuss SCR models that integrate auxiliary information on resource selection obtained by telemetry. Telemetry data are directly informative about the coefficient of the distance term (σ or α_1) which, in fact, can be estimated from telemetry data alone. It stands to reason that, when telemetry data are available, this should affect considerations related to trap spacing. Conceivably even, one might be able to build SCR designs that don't yield any formal spatial recaptures because all of the information about σ is provided by the telemetry data. We have done limited evaluations of the trap spacing problem in the presence of telemetry data, and the results suggest that, while efficient designs that involve telemetry data have a larger trap spacing than without telemetry data, the realization of some spatial recaptures is important even when telemetry data are available. With the **R** code we provide in Chapter 13, you should be able to carry out your own custom evaluation of these types of design problems.

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Non Print Items

Abstract: In the context of spatial sampling problems, where populations of mobile animals are sampled by an array of traps (or other sampling devices), there are a number of critical design elements. Two of the most important ones are the spacing and configuration of traps within the array. In this chapter we recommend a general framework for evaluating design choices for SCR studies, such as trap spacing, using Monte Carlo simulation of specific design scenarios—what we call scenario analysis. We evaluate trade-offs between trap spacing and the total area covered by traps (considerations that are related to available funding and logistics), including designs based on regular, clustered and rotating traps, and show that SCR models are flexible and perform well under a range of spatial design scenarios. While we recommend scenario analysis as a general tool to understand your expected data before carrying out a spatial capture-recapture study, it is possible to develop some heuristics and even analytic results related to the broader problem of model-based spatial design using an explicit objective function based on the inference objective. We outline an approach where we identify a variance criterion, namely, the variance of an estimator of N for the prescribed state-space. An ideal spatial design should minimize this variance. We show that this depends on the configuration of trap locations, and we provide a framework for optimizing the variance criterion over the design space (the collection of all possible designs of a given size).

Keywords: Model-based design, Optimal sampling design, Sample size, Scenario analysis, Spatial design, Spatial sampling, Trap placement, Trap arrangement, Trap spacing