

SAMPLING DESIGN

Statistical design is recognized as an important component of animal population studies (Morrison et al., 2008; Williams et al., 2002). Many biologists have probably 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, conceptual and heuristic design considerations have been addressed by a number of authors (e.g., Nichols and Karanth, 2002, Chapt. 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 have come out (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 your 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 and, hopefully, 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 Jr 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 evaluated 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 \times 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 mean of all 900 grid cells) with good statistical properties,

where the expectation is with respect to 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. Classical design-based sampling does not tell us anything about the specific 100 sample units that we obtained in our sample. However, 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.

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 too. 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 of 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 into the sample (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 as we obtain our sample.

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.

9725 However, in all real animal sampling problems they are unknown because we never know
9726 precisely where each individual lives and therefore cannot characterize its encounter prob-
9727 ability. Therefore, we have to estimate the sample inclusion probabilities using a model.
9728 SCR models achieve this effect formally, using a fully model-based approach based on a
9729 model that accounts for the organization of individual activity centers and trap locations.
9730 This notion of Horvitz-Thompson estimation suggests that perhaps we should consider
9731 designing SCR studies based on the Horvitz-Thompson variance estimator as a design
9732 criterion. We discuss this a little bit later in this chapter.

9733 10.1.3 Focal population vs. state-space

9734 In SCR models we make a distinction between the focal population – the population of
9735 individuals we care about – and those of the state-space, which we are required to prescribe
9736 in order to fit SCR models. These are not the same thing. The geographic scope of the
9737 population of inference is the region within which animals live that you care about in your
9738 study – let’s call this “the study area”. This is often prescribed for political reasons or
9739 legal reasons (e.g. a National Park). To initiate a study, or perhaps motivating the study,
9740 you have to draw a line on a map to delineate a study area, although often it is difficult
9741 to draw this line, and where you draw it is not so much a statistical/SCR issue. On the
9742 other hand, you need to prescribe the state-space to define and fit an SCR model. This
9743 is the region that contains individuals that you *might* capture. This is different from the
9744 study area in most cases. To design a study, you need a well-defined study area, but the
9745 state-space will also be relevant to efficient distribution of traps, and other considerations.

9746 It is helpful to think about this distinction operationally. We define our study area a
9747 priori. As a conceptual device, we might think of this as the area that, given an infinite
9748 amount of resources, we might wall off so that we can study a real closed population.
9749 This “study area” should exist independent of any model or estimator of some population
9750 quantity, i.e., the subject-matter context should determine what the study area is. Given
9751 a well-defined study area, we use some method to arrange data collecting devices within
9752 this study area. The method of arrangement can be completely arbitrary but, naturally,
9753 we want to choose arrangements of traps that are better in terms of obtaining statistical
9754 information from the data we wind up collecting.

9755 Lets face it – it’s quite a nuisance that animals move around and this makes the idea of
9756 a spatial study area kind of meaningless in terms of management in most cases. Wherever
9757 you draw a line on a map, there will be animals who live mostly beyond that line that will
9758 sometimes be subjected to observation in your study. One of the benefits of SCR models
9759 is they formalize the exposure and contribution of these individuals to your study. That
9760 is a good thing. Thus, you can probably be a bit sloppy or practical in your definition of
9761 “the study area” and not worry too much.

9762 With these general concepts of spatial sampling and the sampling of individuals in
9763 mind, we can now turn our attention to more specific aspects of study design in SCR
9764 surveys, namely the spatial arrangement of detectors. We discuss some general concepts,
9765 and then focus on a couple of specific case studies that apply to the Bernoulli observation
9766 model or passive detection devices. The general concepts are surely relevant to other SCR
9767 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 thus being able 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 captureable 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 in or partially in a hole, then it will have a different probability of being captured than an individual whose home ranges 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 the much smaller ocelots (*Leopardus pardalis*). Ocelots also have much smaller home ranges and therefore should 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. Moreover, even when the trap spacing does not result in holes, 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 MMDM (mean maximum distance moved) are used in combination with traditional CR models to obtain density estimates (see Chapt. 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 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 which 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 (the state-space is a part of the model!), even to areas where we can't capture individuals because we happened to not put a trap near them. Conversely, ordinary capture-recapture models only apply to individuals that have encounter probability that is 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 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 a very small number of sites a huge number of times then we can get a lot of recaptures but only very few spatial ones, 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 Gaussian hazard encounter model, 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 $\sigma \times \sqrt{2}$.

In Sec. 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 ($\sigma^* = 5$), a scenario where spaces between traps were large enough to contain entire home ranges ($\sigma^* = 0.5$), and two intermediate scenarios and where sigma was smaller ($\sigma^* = 1$ unit) and larger ($\sigma^* = 2.5$ units) than the trap spacing, respectively. N was 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 4 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 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 when using a trapping 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. Still, the model performed very well.

An important consideration in this simulation study is that all but the $\sigma^* = 0.5$ units

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, define by the input value of movement parameter σ^* . N = number of individuals in the state space; λ_0 = baseline trap encounter rate.

Scenario	Mean	rmse	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

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)

scenarios provided reasonably large amounts of data, including 20+ individuals being captured on the trapping grid. When dealing with real-life animals that are often territorial and may have lower trap encounter rates, a very small grid compared to an individual's home range may result in the capture of few to no 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 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 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.

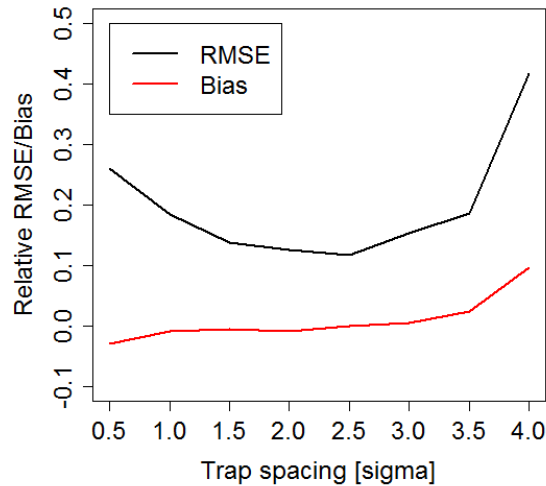


Figure 10.1. Relative bias and RRMSE of estimates of N from an SCR model for a range of trap spacing scenarios.

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., Gardner et al., 2010b; Koehler and Pierce, 2003).

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, only the southern 20% of the traps were retained 10.3.

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

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

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.

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 the 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 which 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 3 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 3 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 that are close to each other in space daily. For example, if you divide your total study area into 4 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 cameras 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 straight forward, as we first demonstrated for the wolverine example in Sec. 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 superior for SCR models than the other, 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 Chapt. 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 (in prep) used a simulation study to investigate different trap arrangements (Fig. 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 3 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 mid-way 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 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 do that.

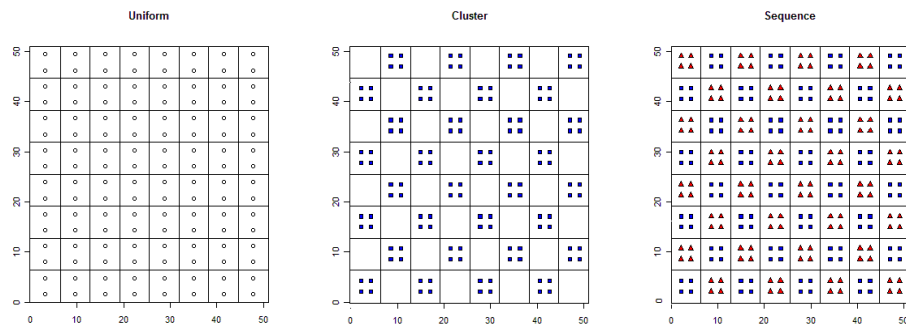


Figure 10.2. Three designs evaluated by Sun (in prep). The left panel shows uniform coverage of the area with traps (hair snares) equally spaced and static for the duration of the period. The central panel shows clusters of 4 traps in close proximity, with larger gaps between clusters. The right panel shows a design in which all grid cells are sampled by the cluster of 4 traps, but in a sequential (in time) manner.

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 also 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. We show that this 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 than 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 do we 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, lets 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:

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

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 1's, 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,

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

Note that the design points \mathbf{x}_j appear explicitly (in the 2nd column of \mathbf{M}). In considering design for estimation in such models it is natural to choose design points, corresponding to values of \mathbf{x} , such that the variance of $\hat{\boldsymbol{\alpha}}$ is minimized. Of course, $\boldsymbol{\alpha}$ 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 a function of 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 $N * J \times 2$ design matrix. The 2nd column of that matrix contains the information about trap locations (the 1st column is still just a column of 1s). Therefore, we could easily find the design \mathbf{X} that optimizes some function of the variance-covariance matrix of the model parameters.

All of this is fine and good if we happen to know the activity centers for each individual. However, this is not a realistic formulation. When \mathbf{s} is unknown, it might make sense to consider minimizing the expected (spatially averaged) variance:

$$E_{\mathbf{s}} \{ \text{Var}(\boldsymbol{\alpha}, \mathbf{X}) \} = \sum_{\mathbf{s} \in \mathcal{S}} (\mathbf{M}'(\mathbf{s}) \mathbf{M}(\mathbf{s}))^{-1}.$$

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 weighs 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: $\mathcal{I}(\boldsymbol{\alpha}, \mathbf{X}) = (\mathbf{M}'(\mathbf{s}) \mathbf{M}(\mathbf{s}))$. 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:

$$\mathcal{I}(\boldsymbol{\alpha}, \mathbf{X}) = \sum_{i=1}^N (\mathbf{M}'_i(\mathbf{s}_i) \mathbf{M}_i(\mathbf{s}_i))$$

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 \mathbf{s}_i we can compute the integrated information,

10109 over all possible values of \mathbf{s}_i , and for *each* \mathbf{s}_i , which is an N -fold summation:

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

10110 which is just N copies of the integrated (spatially averaged) information:

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

10111 It therefore seems sensible to base design of SCR studies on some criterion that is
 10112 a function of this expected information matrix. E.g., find the design that maximizes
 10113 the diagonals, or the determinant, or minimizes the trace of the *inverse* (the variance-
 10114 covariance matrix based on N individuals). This can be done for any number of design
 10115 points $\mathbf{x}_1, \dots, \mathbf{x}_J$ using standard exchange algorithms (see Müller, 2007, Chapt. 3) and
 10116 we discuss this below in Sec. 10.5.5. However, our SCR models are not normal linear
 10117 models but, rather, more like Poisson or binomial GLMs. We see in the next section that
 10118 we can adapt these ideas for such models.

10119 10.5.2 Model-based Design for SCR

10120 Following our development of the normal linear model above, suppose for the moment
 10121 that we know \mathbf{s} for a single individual. In this case, its vector of counts of encounter in
 10122 each trap \mathbf{y} are either binomial or Poisson counts, and the linear predictor has this form:

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

10123 for the Gaussian encounter probability model, or any other model could be used. In vector
 10124 form, we write this as:

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

10125 where \mathbf{M} is the $J \times 2$ design matrix where the 2nd column contains the squared pairwise
 10126 distances between each individual i and trap j , and thus it depends on both \mathbf{X} and \mathbf{s} .

10127 The asymptotic formula for $\text{Var}(\boldsymbol{\alpha})$ can be cooked up for any type of GLM. As an
 10128 example (we use this below), for the Poisson GLM, the asymptotic variance-covariance
 10129 matrix of $\hat{\boldsymbol{\alpha}}$, considering a single individual having location \mathbf{s} , is¹

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

10130 This is a function of the design \mathbf{X} as well as \mathbf{s} both of which are balled-up in the re-
 10131 gression design matrix \mathbf{M} , and the matrix \mathbf{D} which is a diagonal matrix having elements
 10132 $\text{Var}(y_j|\mathbf{s}) = \exp(\mathbf{m}' \boldsymbol{\alpha})$ for y_j = the frequency of encounter in trap j and where \mathbf{m}' is the
 10133 j^{th} row of $\mathbf{M}(\mathbf{s})$. We can compute the expected information under the Poisson model with
 10134 known N using this modified formulation. These ideas are meant to motivate technical
 10135 concepts related to model-based design, where we know N , and therefore have a convenient
 10136 variance or information expression to work with. However, in all real capture-recapture
 10137 applications we won't know N , and so we need to address that issue, which we do in the
 10138 next section.

¹ This 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).

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 capture-recapture studies. For one, we could formulate the objective function based on the variance of the Huggins-Alho estimator (Sec. 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. On the other hand, we find that the calculus is a bit tedious at the present time. As an alternative, we devise a variance criterion based on the conditional estimator of N having the form

$$\tilde{N} = \frac{n}{\hat{p}}$$

where \hat{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, $\hat{\alpha}$. We elaborate on the precise form of \hat{p} and the variance of its MLE below. The variance of this estimator is:

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

An important thing to note is that this estimator, and its variance, are *conditional* on the sample size of individuals, n . We never set out, in capture-recapture, to obtain a sample of n individuals (n is always a stochastic outcome) and so we need to “uncondition” on n . Fortunately, this is a simple proposition using standard rules of expectation and variance, which produce the following expression:

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

The key thing to note about this as a criterion: (1) It depends on \bar{p} , the marginal probability of encounter. Clearly the variance decreases as \bar{p} increases. In general, the form of \bar{p} depends on the SCR model being used. We will provide an example below. Obviously, \bar{p} will depend on the parameter values α . (2) The criterion depends on $\text{Var}(\hat{p})$. So, designs that estimate \bar{p} well should be preferred. This will also depend on the parameters α and *also* the variance of the MLE, $\hat{\alpha}$. Based on these considerations, we suggest a number of appealing 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 n .
- (4) $Q_4 = \text{Var}(\hat{p})$. We should prefer designs which provide good estimates of \bar{p} .

To make use of any of these criteria in a particular design problem, we need to decide on values of N , and the model parameters for computing \bar{p} , and then think about optimizing the criterion over all possible designs (see below).

10.5.4 Too much math for a Sunday afternoon

Here we discuss calculation \bar{p} and variance expressions required to compute the design criteria above.

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, say d_{ij} for the distance between individual activity center \mathbf{s}_i and trap \mathbf{x}_j . Under the Poisson observation model, with a Gaussian hazard model:

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

where here we emphasized that this is conditional on \mathbf{s}_i and also the design – the trap locations \mathbf{x}_j . The *marginal* probability of encounter, averaging over all possible locations of \mathbf{s} is:

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

It is important to note that this can be calculated directly *given* the design \mathbf{X} , and parameters of the model. This is handy because we see that it is used in the variance formulae given subsequently and therefore it is used directly in evaluating any of the criteria described above.

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

Developing an expression for $\text{Var}(\hat{\bar{p}})$ 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). We first express the integral in Eq. 10.5.4 as a summation over a fine mesh of points so that:

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

which under the Poisson observation model is, in a simplified notation:

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

10201 The MLE of $\bar{p}(\mathbf{X})$ has us plug in the MLE of the parameters of the model, in this case
 10202 $\hat{\lambda}_0 = \exp(\hat{\alpha}_0)$ and $\hat{\alpha}_1$. To compute the variance of the MLE of \bar{p} , we note that the variance
 10203 operator can move inside the summation over \mathbf{s} , and the subtraction from 1 doesn't count
 10204 anything, so we have

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

10205 A few applications of the delta approximation and some arm-waving yields the following
 10206 expression for the variance of $\hat{\bar{p}}$:

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

10207 where $\lambda(\mathbf{x}, \mathbf{s}) = \exp(\alpha_0 + \alpha_1 d(\mathbf{x}, \mathbf{s})^2)$ and $\lambda_{\mathbf{s}} = \sum_{j=1}^J \lambda(\mathbf{x}_j, \mathbf{s})$.

10208 Characterizing $\text{Var}(\hat{\alpha})$

10209 The big picture is this: For a given design \mathbf{X} , we can compute $\text{Var}(\hat{\bar{p}}(\mathbf{X}))$ – this is just a
 10210 calculation involving sums over all points in the state-space and design points – provided
 10211 we know the variance of the estimator of α , $\text{Var}(\hat{\alpha})$ and the parameters of the model.
 10212 However, it is not so easy to write down the analytic form of this matrix. Some calculus
 10213 would have to be done on the conditional likelihood (e.g., from Borchers and Efford (2008))
 10214 to figure out the asymptotic form of this matrix. For our purposes, we think it might
 10215 suffice² to approximate the matrix, using the analogous result from a Poisson or binomial
 10216 GLM assuming that N is known, since we have convenient formulas for those (see Eq.
 10217 10.5.2).

10218 The approximate variance given by Eq. 10.5.2 is conditional on the collection of
 10219 activity centers, $\mathbf{s}_1, \dots, \mathbf{s}_N$. To resolve this, we take the approach outlined previously to
 10220 compute the *expected* information obtained from a particular realization of N individuals,
 10221 and invert that result. In particular, the total information for all N individuals is

$$\mathcal{I}(N) = \mathbf{M}'_1 \mathbf{D}_1 \mathbf{M}_1 + \dots + \mathbf{M}'_N \mathbf{D}_N \mathbf{M}_N$$

10222 We can compute the expected information over *all* elements of the state-space, which is
 10223 just N times the average information of a single individual:

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

10224 Putting it all together

10225 For a single design, \mathbf{X} , we need to compute this expected information quantity, invert it
 10226 to get the variance of $\hat{\alpha}$, and then either use that variance matrix in the calculation of
 10227 criterion Q_1 , or else evaluate some other quantities along the way to computing the other
 10228 criteria. We can compute \bar{p} (which is Q_3) for a given design without doing any variance
 10229 calculations. If we use $\text{Var}(\hat{\alpha})$ along with \bar{p} , we can compute $\text{Var}(\hat{\bar{p}})$, which is Q_4 . We can
 10230 combine all of these things together and compute $\text{Var}(\tilde{N})$ for a given \mathbf{X} . This gives us Q_2 .

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

10231 **10.5.5 Optimization of the criterion**

10232 To compute spatial designs that optimize a given criterion, we need to come up with a
 10233 ballpark guess of the model parameters so that the criterion can be evaluated for any
 10234 design. i.e., what are the values of α and N we expect in our study? If we do that,
 10235 and specify the state-space \mathcal{S} then, we can, in theory, optimize the variance criterion
 10236 over all possible configurations of J traps. In formulating the optimization problem note
 10237 that we have J sample locations corresponding to rows of \mathbf{X} . The problem is therefore a
 10238 $2J$ dimensional optimization problem which, for J small, could be solved using standard
 10239 numerical optimization algorithms as exist in almost every statistical computation envi-
 10240 ronment. However, J will almost always be large enough so as to preclude effective use of
 10241 such algorithms. This is a common problem in experimental design, and spatial sampling
 10242 in general, for which sequential exchange or swapping algorithms have been fairly widely
 10243 adopted (e.g., Wynn, 1970; Fedorov, 1972; Mitchell, 1974; Meyer and Nachtsheim, 1995;
 10244 Nychka et al., 1997; Royle and Nychka, 1998). The basic idea is to pose the problem as a
 10245 sequence of 1-dimensional optimization problems in which the objective function is opti-
 10246 mized over 1 or several coordinates at a time. In the present case, we consider swapping
 10247 out \mathbf{x}_j for some point in \mathcal{X} that is nearby \mathbf{x}_j (e.g., a 1st order neighbor). Beginning with
 10248 an initial design, chosen randomly or by some other method, the objective function is eval-
 10249 uated for all possible swaps (at most 4 in the case of 1st order neighbors) and whichever
 10250 point yields the biggest improvement is swapped for the current value. The algorithm is
 10251 iterated over all J design points and this continues until convergence is achieved. Such
 10252 algorithms may yield local optima and optimization for a number of random initial designs
 10253 can yield incremental improvements. We implemented such a swapping algorithm in **R**,
 10254 and it is available as a function in the **scrbook** package with the function **SCRdesign**. The
 10255 algorithm operates on a discrete representation of \mathcal{S} (an arbitrary matrix of coordinates).
 10256 For each point in the design, \mathbf{X} , only the nearest neighbors (the number is specified by
 10257 the user) are considered for swapping into the design during each iteration. For example,
 10258 to compute `ndesigns = 10` putative optimal designs (each based on a random start) of
 10259 size $J = 11$, we execute the function as follows:

```
10260 > des<-SCRdesign(S,X,ntraps=11,ndesigns=10,nn=15,sigma=1)
```

10261 Where the state-space \mathcal{S} , the candidate set \mathbf{X} are provided as matrices, `nn` is the number of
 10262 nearest neighbors to inspect for each design point change, and `sigma` is the scale parameter
 10263 of, in this case, a Gaussian hazard model. See the help file **SCRdesign** for examples and
 10264 analysis of the output.

10265 While swapping algorithms are convenient to implement, and efficient at reducing
 10266 the criterion in very high dimensional problems, they do not always yield the global
 10267 optimum. In practice, as in the examples below, it is advisable to apply the algorithm to
 10268 a large number of random starting designs. Our experience is that essentially meaningless
 10269 improvements are realized after searching through a few dozen random starts.

10270 The design criteria we developed above bear a striking resemblance to design criteria
 10271 used to construct so-called space-filling designs (Nychka et al., 1997). Such criteria are
 10272 based on inter-point distances, and space-filling designs seek to optimize some function
 10273 of distance alone, instead of a variance-based objective function. The benefit of this
 10274 approach is that one doesn't have to specify the model to produce a design, and space-
 10275 filling designs have been shown to provide reasonable approximations to designs based on

variance criteria under flexible statistical models (Nychka et al., 1997). This similarity suggests that perhaps certain distance-based design criteria might be suitable for SCR models. A version of a swapping algorithm used to optimize a space-filling criterion is implemented in the **R** package **fields**.

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 size 11 and 21 were computed using 10 random starting designs. We found the optimal design using each of the 4 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 \hat{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 Fig. 10.3. There are a few points of some interest here.

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 \hat{N} , 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 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 (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 are very regular looking 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 exactly regular, the average closest neighbor distance is not exactly the same as the trap spacing of a regular grid design.

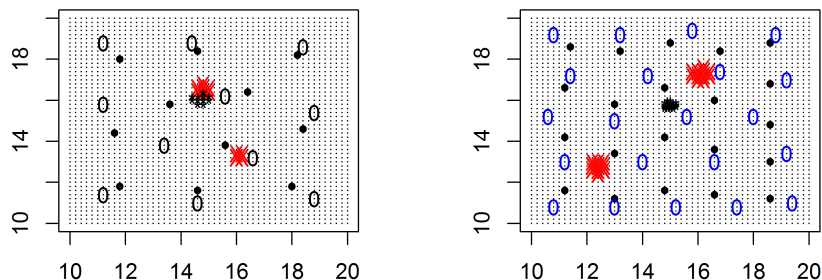


Figure 10.3. Best designs for each of 4 design criteria, produced using the exchange algorithm with 15 nearest-neighbors and based on 10 random starting designs. The left panel shows the best $J = 11$ point designs, and the right panel shows the best $J = 21$ point designs. The solid black dots correspond to the best design for Q_1 , 0 marks the design for Q_3 , "X" for Q_2 and the tightly clustered "*" corresponds to Q_4 .

10318 10.5.7 Density covariate models

10319 Many capture-recapture studies will involve one or more landscape or habitat covariates
 10320 that are thought to affect density, with the idea of using the methods described in Chapt.
 10321 11 for modeling and inference. We imagine that it should be possible to extend the
 10322 model-based framework described previously to accommodate uncertainty due to having
 10323 to estimate β , and this could be included as a feature of the design criterion.

10324 In this case, we can think of the captures in a trap being Poisson random variables
 10325 with mean $\mu(\mathbf{x}, \mathbf{s}) * D(\mathbf{s})$ and we think the same arguments as given above can be used
 10326 to devise design criteria and optimize them. However, in this case we might not only
 10327 care about estimating N but also (or instead) inference about the parameters β . Thus,
 10328 we might choose designs that are good for N or perhaps only good for estimating β or
 10329 perhaps both. Intuitively, we think these two design objectives conflict with one another
 10330 to some extent. Model-based approaches should favor areas of higher density, but the
 10331 design points need to realize variation in the landscape covariates too.

10332 10.6 TEMPORAL ASPECTS OF STUDY DESIGN

10332 The spatial configuration of traps is one of the most important aspects of sampling design
 10333 for capture-recapture studies. Indeed, as we discussed in the previous section, design
 10334 under SCR models can be thought of as being analogous to classical model-based spatial
 10335 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 discuss 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 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 Chapt. 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 Chapt. 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 or immigration from 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. Further, because some individuals are not available for detection for the entire study (they only become available when they are recruited) we would expect 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 actually on the study area, 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 couple of months can still be considered short. In practice, we have no means of ever 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 sec. 10.4) can require even longer sampling to accumulate sufficient captures and recaptures. So clearly, in temporal study design we

10380 have to strive for a compromise between collecting enough data while still approximating
 10381 a closed population. For some species we may be able to avoid seasons where violation
 10382 of demographic closure is particularly likely – for example migration seasons in migratory
 10383 birds, or specific breeding seasons (or collective suicide season in lemmings). But for many
 10384 species such biological seasons might be less clear cut. For example, in warm climates tigers
 10385 and other large cats can breed year round (Nowak, 1999). As a consequence, guidelines
 10386 as to what time frame adequately approximates a closed population are generally vague
 10387 and arm-wavy. Unfortunately, we do not have much more to offer on the subject of how
 10388 to decide on the length of a study, other than to urge you to think about the biology of
 10389 your study species *before the study* and choose a time window that seems appropriate for
 10390 that purpose.

10391 10.6.2 Diagnosing and dealing with lack of closure

10392 Once a field study has been conducted, you may wonder whether the collected data contain
 10393 any evidence that the closure assumption has been met or violated. Relatively few tests
 10394 for population closure in traditional capture-recapture have been developed, mostly due
 10395 to the fact that behavioral variation in detection is indistinguishable from violation of
 10396 demographic closure (Otis et al., 1978; White et al., 1982). Otis et al. (1978) developed
 10397 a test for population closure that can handle heterogeneity in detection probability, but
 10398 does not perform well in the presence of time or behavioral variation in p . Stanley and
 10399 Burnham (1999) developed a closure test for model M_t (time variation in detection), which
 10400 works well when there is permanent emigration and a large number of individuals migrate.
 10401 Both tests are implemented in the program **CloseTest** Stanley and Richards (2013).

10402 There are no specific population closure tests for SCR models, for the same reasons that
 10403 violation of other model assumptions cannot necessarily be distinguished from a lack of
 10404 population closure. If you are worried that closure might have been violated in your study,
 10405 one approach of dealing with this problem is to fit an open population model. You can
 10406 subdivide your study into several periods and fit a spatial version of Pollock’s robust design
 10407 capture-recapture model, which can estimate population size/density for each of these
 10408 periods (in this context also called primary periods) using models of demographic closure.
 10409 Alternatively, we may consider fully dynamic models which contain explicit parameters
 10410 of survival and recruitment (Chapt. 16). These models can be quite time consuming,
 10411 and if you wanted a faster check you could alternatively fit a spatial Cormack-Jolly-Seber
 10412 model that only estimates survival. The magnitude of the survival estimates gives you
 10413 some partial information about population closure in your study – if survival is close
 10414 to 1 at least there is little evidence of losses of individuals, either through permanent
 10415 emigration or death. These and other open population models are presented in detail in
 10416 Chapt. 16. Finally, if your data are too sparse to fit a full-blown open population model,
 10417 you can subdivide your study into $t = 1, 2, \dots, T$ primary periods and estimate abundance
 10418 separately for each period’s worth of data, possibly sharing the detection parameters across
 10419 periods, if you can safely assume they remain constant. You can do that by either letting
 10420 N_t be independent from each other, or by specifying an underlying distribution for all N_t
 10421 in a multi-session framework as described in Chapt. 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, in prep). This takes a lot of time but it guarantees forward progress, or at least not doing the dumbest from among several dumb things. 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 simulate 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.

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. 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 4 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 on the scale of 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 gender or time effects in the black bear example – see also Chapt. 7) into SCR models to obtain density estimates that reflect the actual state of the studied population.

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

The other general strategy for constructing spatial designs is a formal model-based strategy in which we seek the configuration of design points (trap locations) $\mathbf{x}_1, \dots, \mathbf{x}_J$ which are 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

10467 in ecology. In our view, model-based design under SCR models has great potential due
10468 to its coherent formulation and flexibility. On this topic, we have just barely scratched
10469 the surface here, showing how to formulate a criterion that is a function of the design,
10470 and then optimizing the criterion over all possible designs. Our cursory analysis of model-
10471 based design in a single situation did reveal an important aspect of design that has not
10472 been discussed in the literature. That is, the optimal spacing of traps in an array depends
10473 on the *density* of traps in the state-space. In our analysis, the spacing of 11 and 21 trap
10474 optimal designs was quite different. Therefore, this should be considered in practical SCR
10475 design exercises.

10476 Conceptually, the information in SCR studies comes in two parts: Recaptures of in-
10477 dividuals at different traps (spatial recaptures) and the total sample size of individuals.
10478 Maximizing both of these things as objectives induces an explicit trade-off in the construc-
10479 tion of capture-recapture designs. We need designs that are good for estimating \bar{p} and
10480 also designs that obtain a high sample size of n . Designs that are extremely good only for
10481 one or the other will produce bad SCR designs – estimators of density with low precision
10482 – or designs in which N is not estimable due to a lack of spatial recaptures. One possible
10483 exception is when telemetry data are available (or other auxiliary data). In Chapt. 13 we
10484 discuss SCR models that integrate auxiliary information on resource selection obtained
10485 by telemetry. Telemetry data are directly informative about the coefficient of the distance
10486 term (σ or α_1) and, in fact, can be estimated from telemetry data alone. It stands to
10487 reason that, when telemetry data are available, this should affect considerations related to
10488 trap spacing. Conceivably even, one might be able to build SCR designs that don't yield
10489 any formal spatial recaptures because all of the information about σ is provided by the
10490 telemetry data. We have done limited evaluations of the trap spacing problem in the pres-
10491 ence of telemetry data, and the results suggest that, while efficient designs have a larger
10492 trap spacing than without telemetry data, the realization of some spatial recaptures is
10493 important even when telemetry data are available. With the **R** code we provide in Chapt.
10494 13, you should be able to carry out your own custom evaluation of these types of design
10495 problems.