Title

Authors

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1 Abstract

1. There has been an increasing amount of papers that have been producing estimated activity centre distributions -the summed posterior distribution of estimated range centres from a Bayesian fit of a homogeneous Poisson model- and claiming them to be "species distribution models", when this is not the case. In this paper we will demonstrate that these activity centre distributions and predicted density surfaces are not the same.

2. We illustrate this point through simulation and modelling of real data using the **secr** package (**?**). We simulate using a grey scale image of the Mona Lisa, using the intensity of greyscale as the density of the "population". Then simulating from three different arrays on this surface, produce estimated activity centre surfaces and compare to the true density image, using models assuming constant density and models with covariates. We also use camera-trap capture-recapture survey data of snow leopards in South Gobi, Mongolia. We create predicted

density surfaces as well as estimated activity centre distributions to draw comparisons between the two methods.

3. There were very apparent differences in the surfaces produced via simulation and using the snow leopard data. The activity centre distributions are not representative of the predicted density surface using **predictDsurface**. They are very array dependent, even in areas where arrays overlap there are very different surfaces produced. As you move further away from the centre of the array the density also decreases, reflecting the fall in the detection function as you move from the traps.

4. Overall the results produced by these activity centre distributions do not perform very well, the simulations demonstrate very apparent differences from the true density. With the snow leopard data, the results are surprising, producing some results that are not probable.

2 Introduction

Spatial capture-recapture (SCR) models are a set of methods for modelling capture-recapture data obtained from detectors such as camera-traps, hair snag traps and live-capture surveys such that individuals can be identified. Using the location of the detectors (traps) and also the detections of individuals over several occasion (capture histories), a estimate of density of individuals within a population can be obtained as well as an estimate of population size (**?**). In order to do this, a spatial model of the population and a spatial model of the detection process are fitted to the capture histories of detected individuals. This can be done using inverse prediction and maximum likelihood as well as using data augmentation and Markov chain Monte Carlo methods.

SCR combines a state model describing the distribution of activity centres in the landscape and an observation model relating the probability of detecting an individual at a particular detector to the distance from a central point in each animal's home range.

Consider a survey in which K traps are placed in a region containing animals having home ranges with fixed centres (also known as activity centres). Once an animal is caught in a trap it remains there until it is released. These traps are checked at regular intervals and marked in such a way that their complete capture history is known and are released. There are S trapping occasions, trap k is located at Cartesian co-ordinates x_k and the location of traps within the survey are at $x = (x_1, ..., x_k)$. The number of unique animals caught are n. $\boldsymbol{X}$ is the animal's location and this is it's activity centre.

Let $\omega_i = 1$ if animal i was captured on any of the s occasions and 0 if otherwise. If animal i was captured on trap k on occasion s $(s = 1, ..., S)$ then $\omega_{is} = 1$ and 0 otherwise. The capture history for animal i is $\omega_i = (\omega_{i1}, ..., \omega_{iS})$. Let $p_{ks}(\boldsymbol{X}; \boldsymbol{\theta})$ be the probability that an animal with activity centre at x is caught in trap k on occasion s, where $\boldsymbol{\theta}$ is the capture probability parameter vector.

From (**?**) the likelihood is the joint distribution of the n animals captured and their capture histories $\boldsymbol{\omega}_1, ..., \boldsymbol{\omega}_n$ is

$$L(\boldsymbol{\phi}, \boldsymbol{\theta} | n, \boldsymbol{\omega}_1, ..., \boldsymbol{\omega}_n) = Pr(n | \boldsymbol{\phi}, \boldsymbol{\theta}) Pr(\boldsymbol{\omega}_1, ..., \boldsymbol{\omega}_n | n, \boldsymbol{\theta}, \boldsymbol{\phi})$$

θ is the vector of capture function parameters and ϕ is a vector of parameters of the spatial point process governing animal density and distribution.

When activity centres occur according to a homogeneous Poisson process with rate parameter D, the likelihood is simplified to

$$L(\boldsymbol{\theta}, D) = \frac{Da(\boldsymbol{\theta})^n exp^{-Da(\boldsymbol{\theta})}}{n!} \times \binom{n}{n_1, ..., n_C} \prod_{i=1}^{n} \frac{\int Pr(\boldsymbol{\omega}_i|\mathbf{X};\boldsymbol{\theta})d\mathbf{X}}{a(\boldsymbol{\theta})}$$

where

$$Pr(\boldsymbol{\omega}_i|\boldsymbol{X};\boldsymbol{\theta}) = \prod_s \prod_k p_{ks}(\mathbf{X};\boldsymbol{\theta})^{\delta_k(\boldsymbol{\omega}_{is})} 1 - p_{.s}(\mathbf{X};\boldsymbol{\theta})^{1-\delta_{.}(\boldsymbol{\omega}_{ks})}$$

and $a(\boldsymbol{\theta}) = \int p_{.}(\mathbf{X};\boldsymbol{\theta})d\mathbf{X}$. An estimate of density can be obtained from the MLE estimate of $\hat{\theta}$ and hence $\hat{a}(\hat{\boldsymbol{\theta}})$ from the conditional likelihood, D is then estimated from $\hat{D} = n/\hat{a}$. If the capture probability and a depend on covariates such as $\boldsymbol{z}$ then $\hat{D} = \sum_{i=1}^{n} \hat{a}(\boldsymbol{z_i})^{-1}$. D is a fn of covariates, log link it, and also can do splines

By using the estimates of the density model parameters ϕ we can estimate the probability density function of animal home-range centres in area A: $\hat{\pi} = \hat{D}(\hat{X})/\int_A \hat{D}(\boldsymbol{X})d\boldsymbol{X}$. Given individual i's and it's capture history $\boldsymbol{\omega}_i$ and an estimate of the capture probability parameter vector $\boldsymbol{\theta}$, the probability density function of $\boldsymbol{X}$, the location of this individual's home range centre (activity centre).

$$\hat{f}(\boldsymbol{X}_i|\boldsymbol{\omega}_i) = \widehat{Pr}(\boldsymbol{\omega}_i|\boldsymbol{X}_i)\hat{\pi}(\boldsymbol{X}_i)/\int_A \widehat{Pr}(\boldsymbol{\omega}_i|\boldsymbol{X})\hat{\pi}(\boldsymbol{X})d\boldsymbol{X}$$

And for a homogeneous Poisson process this simplifies to:

$$\hat{f}(\boldsymbol{X}_i|\boldsymbol{\omega}_i) = \widehat{Pr}(\boldsymbol{\omega}_i|\boldsymbol{X}_i)/\int_A \widehat{Pr}(\boldsymbol{\omega}_i|\boldsymbol{X}))d\boldsymbol{X}$$

In several papers, there has been some confusion as to the difference between estimated activity centre distributions- the summed posterior distribution of estimated range centres from a Bayesian fit of a homogeneous

Poisson model - and density surfaces (**????**). with the former even being referred to as a "species distribution model" (**?**) and states that this approach is useful even when the sources of spatial variation in population density are not known. In this paper we will illustrate that the two are not equivalent. There are various problems with interpreting these surfaces as "species distribution models" and "density surfaces", attention is only focused on individuals that were caught. The individuals that were not caught but were present are represented by a smoothly varying base level that dominates the outer regions of the plot. The surface also depends on sampling intensity, as more data is added the the surface will change shape systematically and the plots are prone to artefacts (**?**).

3 Materials and methods

Estimated density surfaces and activity centre distributions are usually presented as images, these being easier to absorb and interpret. In order to present our argument and results in a way that is easy to interpret we also largely present our results as images.

3.1 Simulating a binomial point process

We simulate a fixed number of animals distributed across a single dimension according to a linear trend, and then model this data using a binomial point process that incorrectly assumes a uniform distribution of animals across space. Here one can think of, for example, a situation in which true density strongly depends on a covariate that varies in space, but that this covariate is unknown.

We place a fixed number of points N at random locations on the interval $0 < x < R$, with $R = 15$. Points are generated according to a probability density that makes them more likely to appear near $x = 0$ than $x = 15$ i.e. $f(x) \propto 1 - x/15$ for $0 < x < 15$ and $f(x) = 0$ otherwise.

For simplicity we divide the interval into $R = 15$ equal-sized regions, thinking of these as cells in a one-dimensional grid. Traps are placed in $T = 5$ cells. We make the simplifying assumptions that animals do not move from the cell they are placed in, and that each trap detects animals perfectly within the cell it occupies but cannot detect animals beyond that cell.

We simulate with $N = 50000$ animals and with different trap configurations.

3.2 Simulating a Poisson point process

We simulate data from a density surface model based on one of the most recognisable images in Western culture, the Mona Lisa. We created a greyscale version of a region of the original image (Figure **??**, "Original") and down-scaled this to 50x50 pixel resolution (Figure **??**, "Low Res"). The greyscale value in each cell of the "Low Res" gives the true density of activity centers in that cell, with lighter areas indicating higher densities.

We then used the density surface in the "Low Res" image to generate two realisations of points from the underlying process. In the first of these we generated the number of points from a single draw from a Poisson distribution with mean 7500, resulting in 7451 activity centers being generated. These represent the true activity centers in our study region (Figure **??**, "Simulated"). This realisation has the advantage of closely reproducing the source image, thereby giving the estimated density surface every opportunity to do the same, but is also much larger than the number of centers that would typically be present in a wildlife survey. We therefore also generated a much smaller second realisation of 84 points (Figure **??**, "Simulated small"). This realisation clearly no longer captures the Mona Lisa, but is a more useful aid to understanding some aspects of SCR models.

Figure 1: Input data for the Mona Lisa simulation study. From a grayscale version of the Mona Lisa ("Original"), we created a downscaled 50x50 pixel version ("Low Res") that represents the true underlying intensity surface and gives the long-run density of activity centers in each cell. We used this surface to generate a single realization of 7451 activity centers ("Simulated") and 84 activity centers("Simulated Small"); in wildlife survey terms this image represents the density of the activity centers of all animals present in the study region.

3.3 Simulating capture histories

We conducted various simulated surveys of the population, using different arrays of detectors and also varying the number of detection occasions. Different arrays and detection functions were used for the large and small realisations described above. With a large number of activity centers, we simulated capture histories using a half-normal detection function with g_0, the probability of detection at a single detector placed in the centre of the home range, set to 0.5, and σ, the spatial scale parameter, set to 2. We used four different 3x4 arrays (Figure **??**), with array centers $(19, 21)$, $(19, 33)$, $(28, 21)$, or $(28, 33)$. All arrays were spaced such that they have length 8 in the x-plane and 12 in the y-plane, and so have an average spacing of $4 = 2\sigma$. We then simulated a capture history for either one or 20 occasions on each array.

When using relatively few activity centers, visual interpretation was made easier by increasing the spatial scale parameter, effectively increasing the distance animals travel from the activity centers, and also by increasing the distance between detectors. For these cases, we increased σ to 4, holding other detection function parameters at their previous values, and used a 3x4 array centered on $(18, 34)$ and with an average spacing of 8 between detectors, double that used previously. We simulated capture histories after one, three, ten, and 20 occasions.

After simulating these capture histories for these arrays, we then created an estimated activity centre surface for each of these simulations. In this scenario we assumed a model with constant density and compared the resulting estimated activity center surface to the true population density surface.

The next step was to introduce covariates into our density model and see how this affected the estimated surfaces. We generated covariates by manipulating the “Low Res” image to obtain further images using simple image processing operations like blurring and shifting. Covariates are thus all functions of the true densities but the strength of the association between the covariate and true density varies substantially. We generated four covariates: a “strong” covariate that uses a Deriche (blur) filter with a small range, effectively smoothing the image locally; a “moderate” covariate that uses the same blur filter but with a larger range, increasing the amount of smoothing; a “weak” covariate that uses the same degree of blurring as the moderate covariate but in addition shifts the image down and to the right, destroying much of the relationship between covariate and density; and a “locally strong” covariate, which uses the strong covariate values in the top right hand part of the image and the weak covariate values in the remainder of the image. These covariates are shown in the first row of plots in Figure **??**.

We simulated capture histories and created an estimated activity centre or “space use” (including movement) surface for each of these simulations and compared them to the true population density surface. All computations were done using the *secr* package in R version 3.4.3.

3.4 Camera-trap survey of tigers in Nagarahole, India

We reanalysed data obtained from a camera trap survey of tigers *Panthera tigris* living in and around the Nagarahole Tiger Reserve of Karnataka, India, as reported in **?**. A full description of the survery can be found in the original reference. The original survey used a spatial array of 162 motion-activated camera traps, these being placed at 23 km intervals throughout the area (Figure **??**, “All traps”).

We reanalyzed this data in a likelihood-based framework, first with a model assuming constant density and with three different trap arrays. The first array was the same one employed in the original study. The second was a subset of traps that excluded a large number traps in the interior of the study region, thus leaving a substantial part of the study area unsurveyed (Figure **??**, “Subset #1”). The third used another subset of traps that excluded eight detectors from each of two interior areas of the survey area in which the original survey showed the density of activity centers to be particularly high (Figure **??**, “Subset #2”).

We then fitted a number of covariate models in which density was assumed to depend on longitude and latitude. We fitted a variety of linear and smooth functions for each of longitude and latitude; the model selected by the AIC was one including a linear effect of latitude only, and we report results from this model only. Finally, we generated space use densities for constant density model with all traps.

4 Results

4.1 Estimated activity centre surfaces from a 1-D binomal point process

Figure **??** shows the expected number of activity centers for $N = 50000$ animals distributed according a binomial point process with density decreasing linearly with x. Under the extremely simplified conditions of this example (no movement of animals, perfect detection within cells), SCR recovers the true number of activity centers in each cell that contained a detector, knows how many animals were *not* detected[1], and distributes the activity centers of these undetected animals evenly across the cells that do not contain a detector[2].

4.2 Estimated density surfaces when there are many activity centers

4.2.1 Model with constant density

The same patterns hold in two dimensions under the standard wildlife survey assumptions of Poisson-distributed activity centers (with constant intensity) and detectability inversely related to distance from activity center (Figure **??** and **??**). A single sampling occasion was sufficient to capture the broad features of the Mona Lisa, but only close to where detectors were located (Figure **??**, first row). Away from the detectors the estimated density quickly reverted to close to the estimated mean intensity of the process. Additional sampling occasions resulted in the density of activity centers close to detectors being estimated in much greater detail, but did not affect the surface away from detectors (Figure **??**, first row).

[1] Here this is because N is known but if N is unknown it can be estimated. A model assuming a constant density and detecting n animals from a perfect survey of T/R of the study area estimates the total number of animals to be $\hat{N} = n/(T/R)$, implying there are $\hat{N} - n$ animals in the area that were not detected by any trap.

[2] $\hat{N} - n$ activity centers distributed uniformly between $R - T$ trapless cells gives a mean of $(N - n)/(R - T)$ activity centers per cell, close to the mean of the underlying process N/R when $n \ll N$ and $T \ll R$, as would usually be for wildlife surveys.

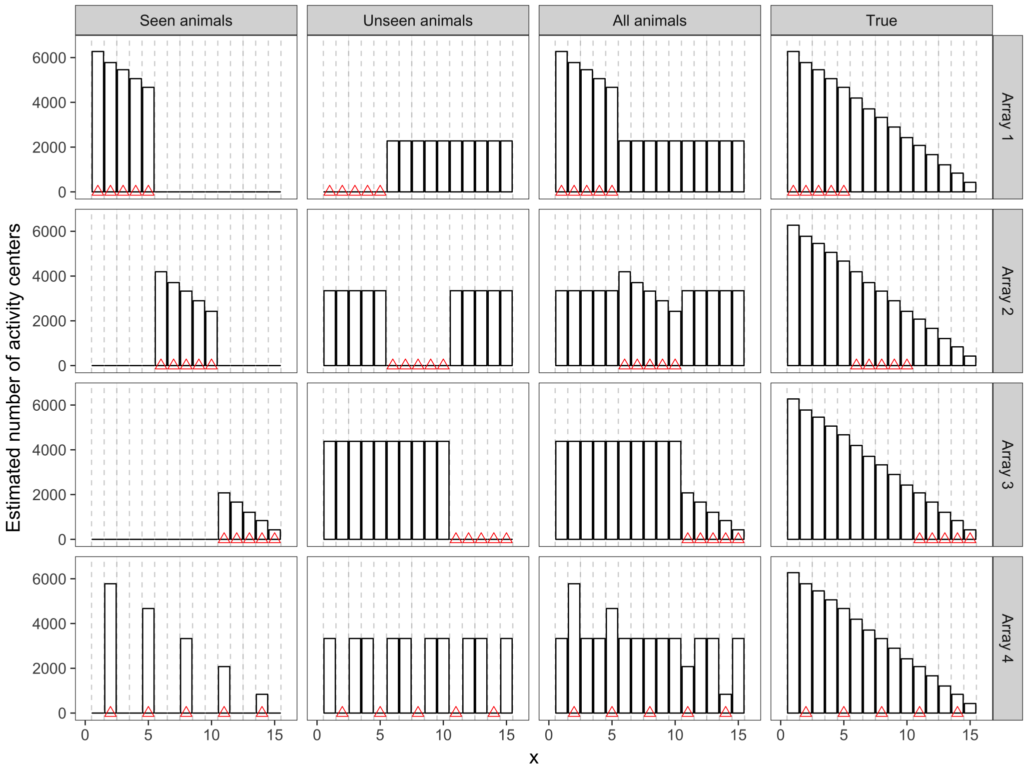

Figure 2: Estimated numbers of activity centers obtained from a binomial point process with $N = 50000$ simulated animals and density decreasing linearly with x, no animal movement, and a step detection function that is perfect within cells and zero otherwise.

Very different relative and absolute densities were obtained depending on where traps are located, even when estimating density *in exactly the same region of the surface and where that region is close to the array* (Figure **??** and **??**, second row). With a single occasion, density was always estimated to be highest nearest the corner where the trap is located (Figure **??**, second row). This pattern occured because the inset region happened to occur in an area of above average density. If instead it occured in a low density region one would see the opposite pattern – low density in the corner containing a trap, increasing away from the trap. This was clearly visible when a single sampling occasion was used, because the estimated surface reverted quickly to the mean intensity. Additional sampling allowed fine detail in the density surface to be estimated close to traps, with slower reversion to mean intensity, but there was still very clear disagreement between the density surfaces returned by the different arrays (Figure **??**, second row).

4.2.2 Model with density depending on covariates

Introducing covariates into the density models allowed us to recover features of the Mona Lisa across the entire image, not just near where detectors were located, although good estimation of activity center locations depended heavily on the availability of good covariates (Figure **??**). With our "strong" covariate we recovered all of the broad features of the Mona Lisa, and many of the fine scale features such as eyes, shading of clouds, *etc.* With the "moderate" covariate we recovered broad scale features but no finer details. With a "weak" covariate, the estimated density surface essentially reverted to the mean intensity of the process across the entire region. With a "locally

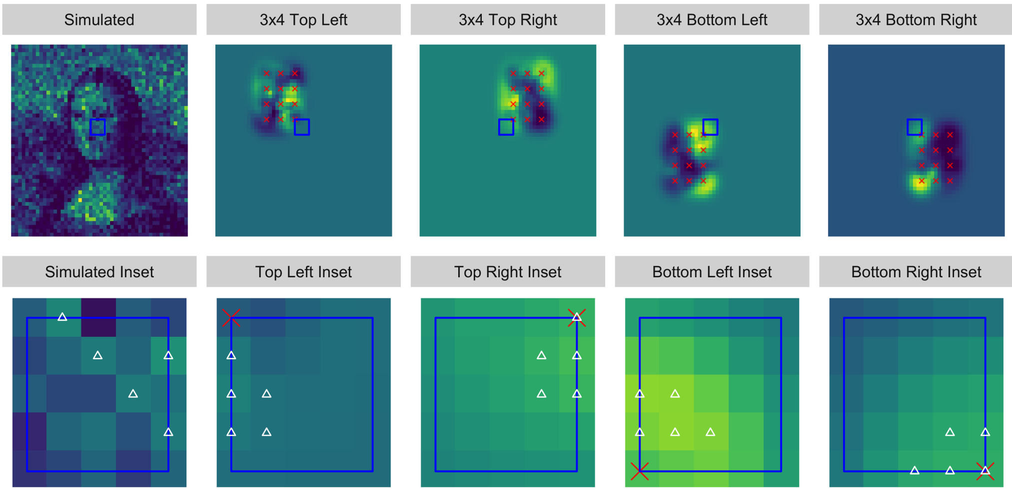

Figure 3: True activity center densities in this realisation ("Simulated") compared with activity center surfaces estimated using different arrays after a single sampling occasion. High density areas are indicated in yellow, low density areas in blue. Detectors are shown as red crosses. Blue squares show the same 4x4 square centered at $(25, 29)$, whose vertices are corner detectors from each of 3x4 arrays. Each plot in the second row shows an enlargement of the blue square in the plot above it. White triangles denote the five cells with the highest estimated densities in each of the second row plots.

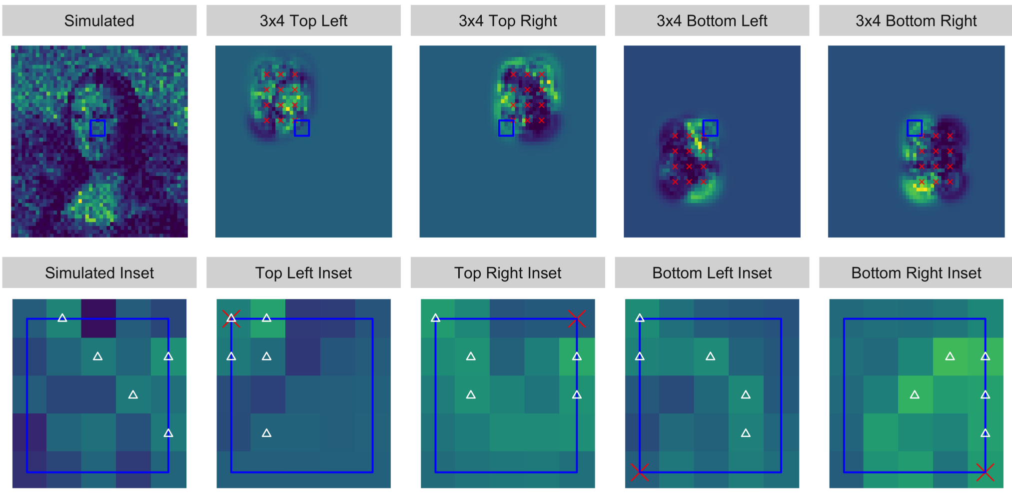

Figure 4: True activity center densities in this realisation ("Simulated") compared with activity center surfaces estimated using different arrays after 20 sampling occasions. High density areas are indicated in yellow, low density areas in blue. See the caption to Figure **??** for further annotation details.

strong" covariate – one that is a good indicator of density in some parts of the study region but poor elsewhere – the dependency on array location was reintroduced. If the array was located where the covariate was strong, the estimated density surface was accurate in that vicinity. If the array was located where the covariate was weak, then the model estimated no relationship between covariate and density and reverted back to the mean intensity everywhere in the region (Figure **??**).

4.3 Estimated density surfaces when there are few activity centers

4.3.1 Model with constant density

We observed similar patterns under the more "wildlife survey appropriate" condition in which we generated only 85 activity centers across the study region (Figure **??**). In this case there is a large difference between the mean intensity surface (the Mona Lisa) and the activity center surface in this realization (85 points), and so it is not surprising that the estimated activity center surface looks nothing like the Mona Lisa (Figure **??**, first row). Nevertheless, a model assuming constant density gives increasingly accurate estimates of the locations of activity centers in the vicinity of detectors as survey effort increases, but very little information is obtained elsewhere, and this does not change with survey effort (Figure **??**, first row). This gives the estimated activity center surfaces a characteristic pattern – the surface becomes increasingly peaked or "spiky" around detectors as survey effort increases, but remains flat away from the array.

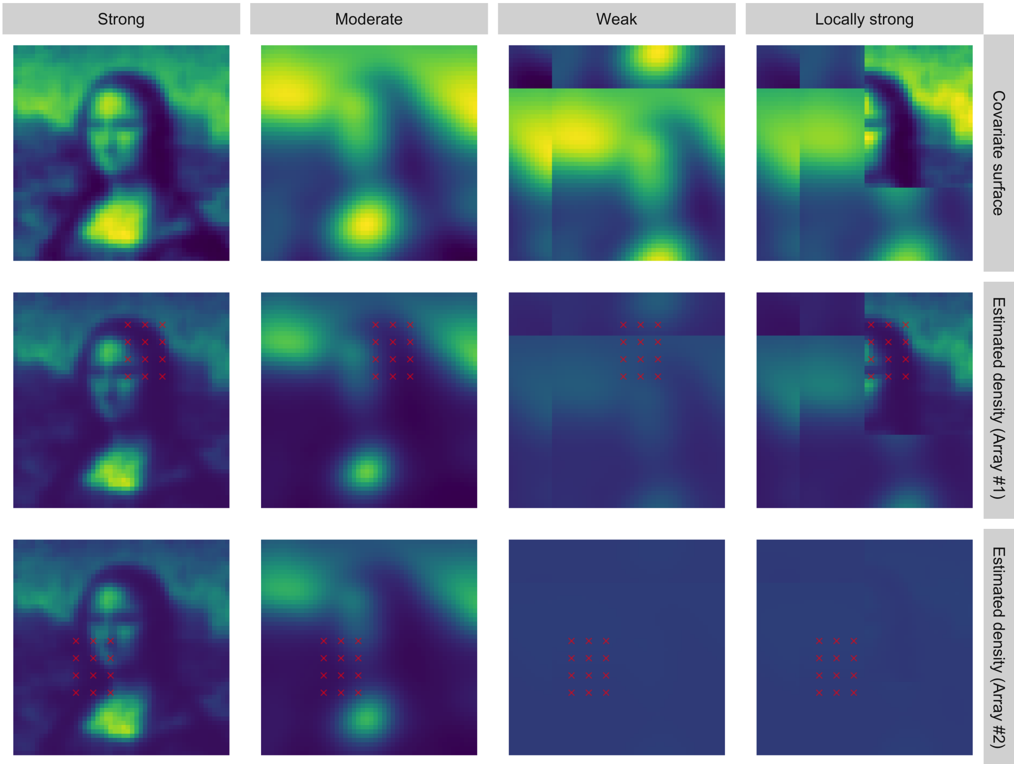

Figure 5: Intensity surfaces estimated using a model with density a function on one of four simulated spatially-varying covariates. Covariates are shown in the first row of plots, and were generating by manipulating the true intensity surface (Figure **??**, "Low Res") by blurring and shifting operations (see Section **??** for details). High density areas are indicated in yellow, low density areas in blue. Detectors are shown as red crosses.

4.3.2 Model with density depending on covariates

Any covariate model returns a surface that is some multiple of the covariate surface. Whether this is a good approximation of the true mean intensity surface depends on the strength of the covariate and sample size. With a strong covariate and sufficient sampling occasions we recovered the Mona Lisa, but with only a single occasion the direction of the relationship was incorrectly estimated, so that dark areas were predicted as light and light areas as dark (Figure **??**, second row). This error was corrected by additional occasions. The same pattern occured with a moderate covariate, but the effect of the weaker covariate is clear in that we did not recover as good an approximation of the Mona Lisa (Figure **??**, third row). Additional sampling would not help with this. Note that in both cases the surface we recovered is an approximation of the mean intensity surface. It does not give a good approximation to the locations of the 85 activity centers in this particular realization.

4.3.3 Space use density surfaces

Space use density surfaces – those that incorporate animal movement – were smoother than the density surface of estimated activity centers and also less sensitive to survey effort (Figure **??**). The space use surface adds a movement kernel that is insensitive to surface effort to an activity center surface that becomes more peaked as survey effort increases, so this is to be expected. Space use density surfaces were not "just" smoothed versions of the activity center surfaces, however. In our example unobserved animals were estimated to be spending their time on the outskirts of the study region, far away

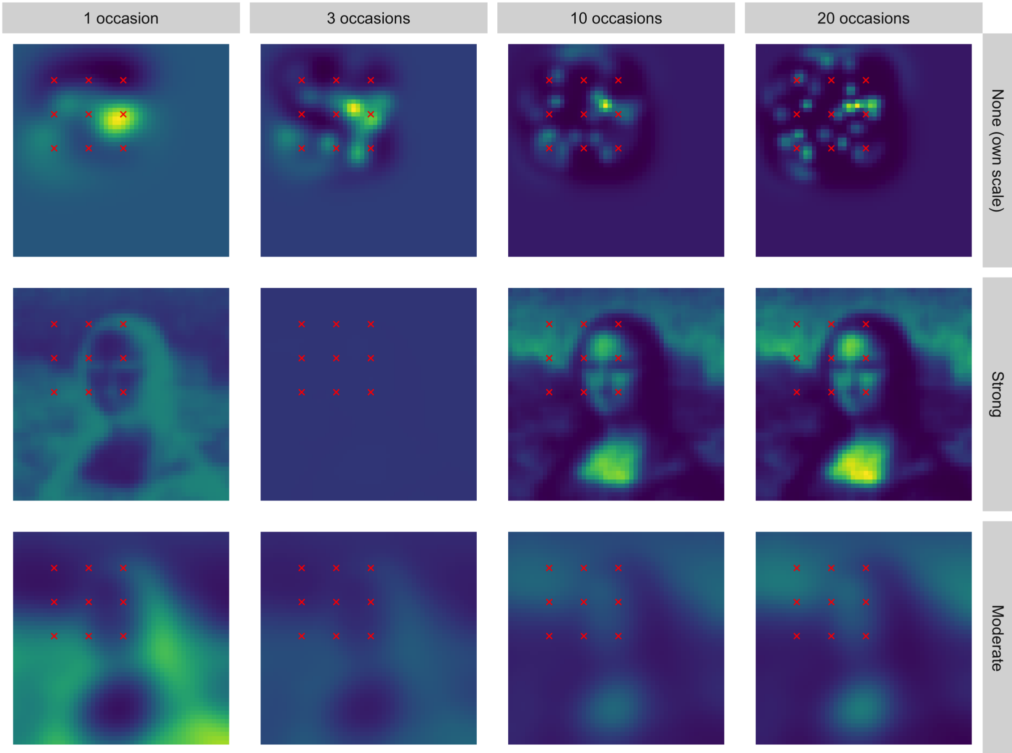

Figure 6: Estimated activity center surfaces from a constant density model (first row) and estimated intensity surfaces from a model with density depending on "strong" or "moderate" covariates (second and third rows respectively, see Section ?? for details of how covariates were simulated). 85 activity centers were generated across the entire image, drawn from a Poisson process with intensity given by the "Low Res" image in Figure ??. High density areas are indicated in yellow, low density areas in blue. Detectors are shown as red crosses.

from any detectors (Figure **??**, second row), which is quite different from the homogenous surface we obtained away from detectors when looking only at activity centers (Figure **??**, first row). In contrast, the space use density surface for captured animals *was* essentially a smoothed version of the activity center surface around the detector array, and so very similar in terms of the broad patterns it showed (Figure **??**, third row).

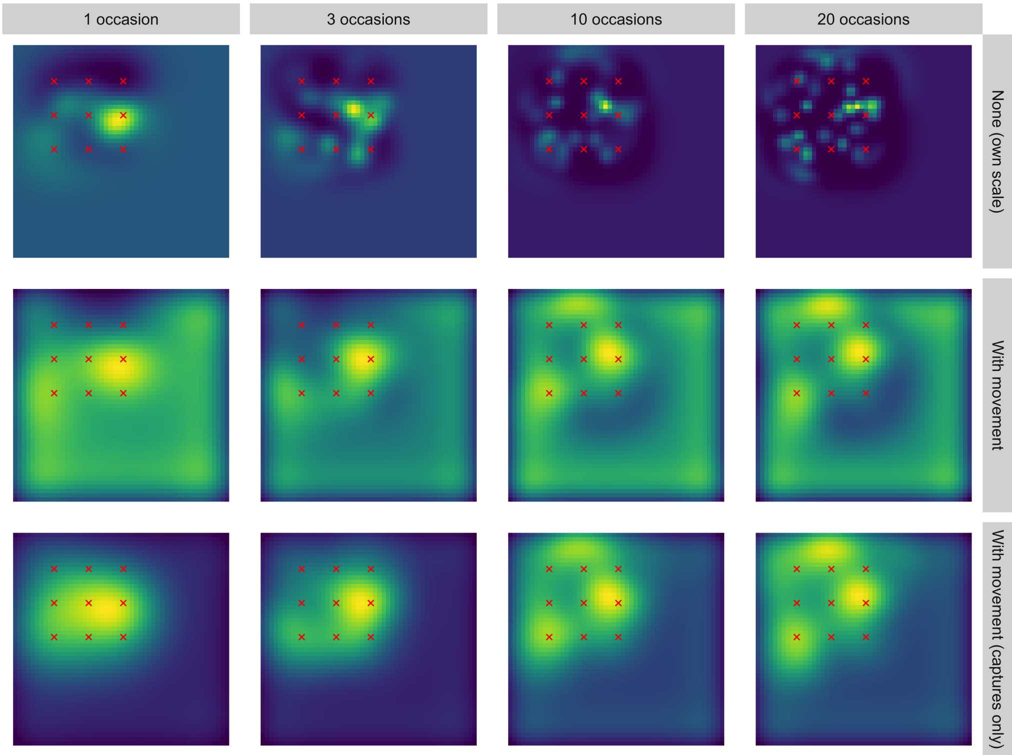

Figure 7: Estimated activity center surfaces from a constant density model (first row) and space use density surfaces incorporating animal movement for both observed and unobserved animals (second row) and for observed animals only (third row). High density areas are indicated in yellow, low density areas in blue. Detectors are shown as red crosses.

4.4 Nagarahole Tiger Sanctuary camera-trap survey

The same broad patterns were visible in our reanalysis of the Nagarahole tiger survey (Figures **??** to **??**).

4.4.1 Model with constant density

The full array of traps used in the original Nagarahole study clearly showed three areas of high activity center density in the interior of the study region, along $E \approx 625$ and $N = 1324, 1330, 1336$ respectively (Figure **??**, "All traps, no cov.").

When we reran the survey on a subset of traps that excludes traps in the interior of the study region, high density areas in the interior of the region were replaced by a flat surface indicating a homogenous low density, and the three high density regions described above were not detected (Figure **??**, "Subset #1, no cov."). We also observed some regions where estimated density *increased* after the removal of the interior traps (see the easternmost detectors in Figure **??**, "Subset #1, no cov."). This occurs when animals have their activity centers near to, but outside, the area circumscribed by an array – estimated activity centers then tend to be pulled towards the traps that they are closest to.

With the second subset of traps, which exclude eight detectors from each of two high density interior areas, the constant density model still recognized that activity centers are located in these areas, but the estimated locations of these activity centers showed a clear shift from what was found in the original survey (Figure **??**, "Subset #2, no cov."). The estimated location of the northernmost of the two activity centers moved to the south east, while the other activity center moved to the south.

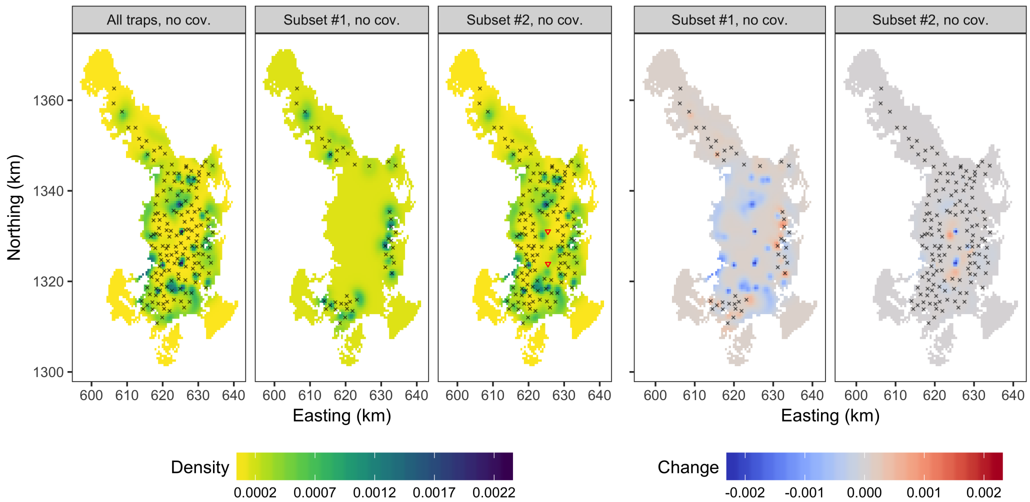

Figure 8: Estimated activity center densities of tigers in Nagarahole Tiger Sanctuary, India, obtained using different camera trap arrays. Plots (a), (b), and (c) show estimated densities; plots (d) and (e) show differences between the estimated densities obtained using using trap subset #1 and #2 and those obtained using all traps. Detectors are shown as black crosses.

4.4.2 Model with density depending on covariates

The model with the lowest AIC was one expressing mean intensity as a linear function of latitude. The estimated density surface obtained from this model showed the estimated mean intensity increasing southwards across the region, with mean intensity in the extreme south roughly four times that in the extreme north (Figure **??**, "All traps, northing"). Estimates of mean intensity were much less variable than estimates of activity center densities, and were also less sensitive to changes in the array of traps, provided that the array provided sufficient coverage of the covariate space to estimate the covariate relationship (Figure ??, "Subset #1, northing" and 'Subset #2, northing").

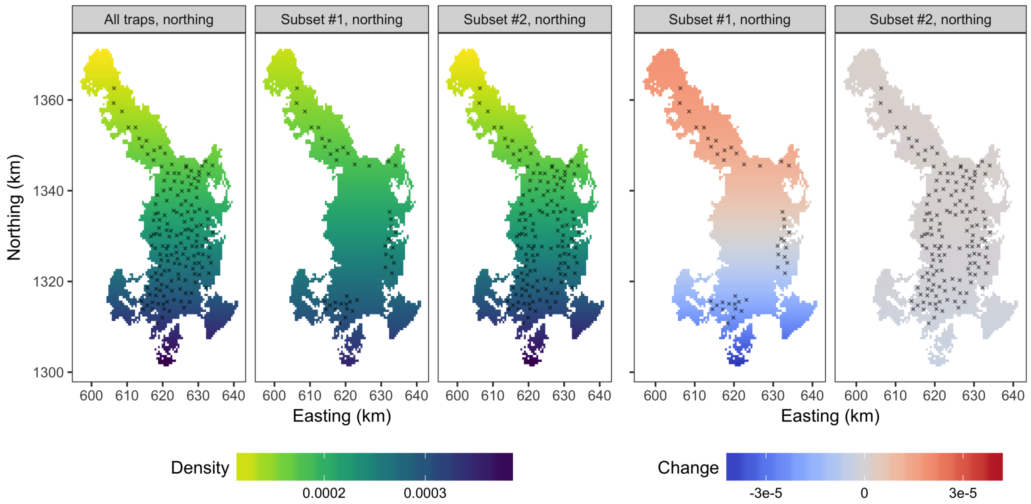

Figure 9: Estimated mean intensity of tigers in Nagarahole Tiger Sanctuary, India, obtained using different camera trap arrays. Plots (a), (b), and (c) show estimated intensities; plots (d) and (e) show differences between the estimated intensities obtained using using trap subset #1 and #2 and those obtained using all traps. Detectors are shown as black crosses.

4.4.3 Space use density surfaces

The estimated space use density surface differed markedly from the activity center density surface, with these differences neatly illustrating the different purposes of the two surfaces (Figure ??). Activity center densities were highest in those cells where sufficient information had been gathered to precisely identify where a single tiger's activity center was. Adding movement to the surface had the effect of dispersing each area of high (activity center) density across a much wider area, the extent of which depended on the estimated range of movement. The estimated spatial scale parameter for the fitted half-normal detection function we used was $\sigma = 1.85$km, so that animals can move a substantial distance from their activity centers, relative to the size of the study area. As a result, space use density was highest in areas in which there were several activity centers in relatively close proximity to one another, even if the location of these activity centers was less precisely known than other activity centers. This occured in areas near the southern and south-western borders of the reserve, as well as in a central location near $N = 1340$ (Figure **??**). In contrast, space use density was low in areas that contained only a single activity center, even if the location of the activity center was precisely known (for example at $N = 1330$, $E = 624$).

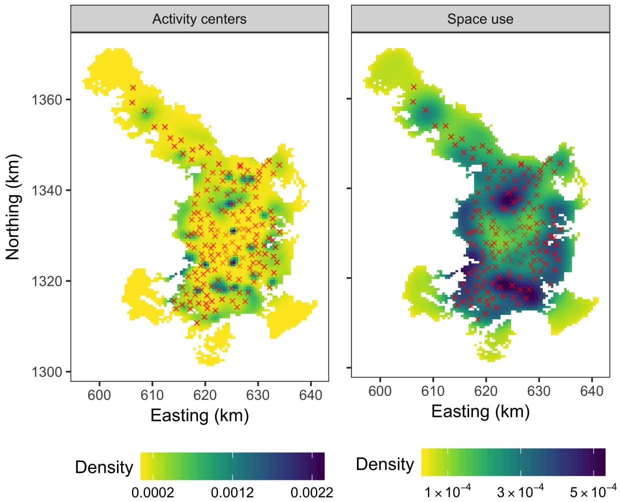

Figure 10: Estimated (a) activity center surfaces from a constant density model and (b) space use density surfaces for tigers in Nagarahole Tiger Sanctuary, India. High density areas are indicated in blue, low density areas in yellow. Detectors are shown as red crosses.

5 Discussion

The activity centre density obtained from an SCR model cannot be interpreted as a species distribution model. Species distribution models predict where species are likely to occur by correlating environmental covariates with species occurrence or species density. Their rationale is to find favourable habitats and predict that animals will be found in similar habitats across the study region. A species distribution model will tend to place higher densities at locations where environmental covariates are most favourable, and spatial variation in the density surface will depend mostly on how environmental covariates change across space.

In contrast, the density on an activity center surface is often placed in spikes where the model is most certain that an activity center is located. The shape and location of these spikes depends on where traps are located and also on survey effort. Different arrays produce different results and these results can be improbable, in the sense that high density spikes can occur at locations in unfavourable habitats, if there happen to be activity centers at these locations at the time of the survey. A useful metaphor here is of SCR as a torch shining a light onto the true activity center density surface – what you see depends on where you shine the torch (trap locations) and how brightly you shine it (survey effort).

More important for people actually conducting SCR surveys is that the densities obtained close to traps (and even inside the trap array) *also* depend on where traps are located. The inset plots of Figure **??** and **??** show the same region in space, and this region lies within a 2.5σ range of all trap arrays, where one would expect to be making inferences about activity centers. We obtained very different density surfaces in this area depending on where traps were located. If one was using SCR to identify areas of high density e.g. for conservation purposes, or to locate animals, different areas would be identified depending on which array was used.

SCR models answer the question "where is an animal with *this* spatial capture history likely to have its activity center?" The answer is always contingent on where traps are located. Changing the locations of detectors also changes the capture history, and thus the answer to the question of where the activity center is located. This occurs regardless of whether one works in a Bayesian or frequentist framework. Precisely the same is true of the estimated activity center density surface, which simply sums estimated activity centers across animals. In this case the question being addressed is "where are the animals with *these spatial capture histories* likely to have *their* activity centers?" The dependency on trap location applies to activity centers estimated for detected animals and for those that were not detected. In the latter case we have limited information and our estimates thus become "nowhere near where traps are located".

None of this precludes activity center surfaces from being useful sources of information, but they do need to be interpreted with care. For practical purposes this means always interpreting them with the caveat that they depend on where traps are located. Activity centre distributions do not give proper answers to questions like "where are the high- and low-density regions?" because the highest and lowest points of the surface will always be at or near traps; not because these are high- or low-density regions of space, but because this is where the capture histories make us most certain that animals are, or are not, present.

When estimating the location of a given activity center, the bias caused by trap locations is lowest if the activity center occurs near the center of a dense array of traps, and is highest if traps are all on one side of the activity center or if detections are only made at a single trap. Thus bias can be reduced by using a design that makes it likely that all activity centers in the study region are surrounded by a network of traps. This will be unachievable for most wildlife surveys, as it requires a large number of traps covering an area beyond the study region, and ideally placed at random *[[[note: I say 'beyond the region' so that activity centers at the borders are also in the center of some array, but not sure this is correct – ????]]]* . In summary, it is incorrect to interpret the activity center density surface as if it indicated where animals currently have their activity centers.

There is a way of using SCR so that it can be interpreted as a species distribution model – by modelling the mean intensity of the underlying process as a function of enviromental covariates. Covariates allow one to see beyond the spatial extent of the array (see Figure **??**), provided that the relationship between covariate and response is a good one, and that traps cover a sufficient range of covariate values to estimate that relationship. The resulting surfaces are no longer tied to one particular realisation of the Poisson process, and thus carry less information about where current activity centers are located. Rather, they show the mean intensity of the underlying process assumed to generate activity centers; in other words, the estimated density of activity centers across all realisations. Density will be highest where environmental covariates are most favourable (such as further south in Figure **??**). They thus answer the question of "where are the high- and low-density regions?" in a way that is consistent with how this question is answered by species distribution models. They predict where we would expect to see activity centers, if we were able to observe multiple independent populations distribute themselves across the study region. The extent to which this surface predicts where animals have their activity center *in this realization* depends on the strength of the covariate relationship and on the number of activity centers, each of which is an independent draw from the underlying process. In the Nagarahole survey, for example, there is a relatively weak northing covariate and a small number of activity centers, and the estimated mean intensity surface provides very little information about the precise location of current activity centers.

The concept of an activity center is central to SCR models, but for many applications of SCR it may be more appropriate to consider a distribution of space use, taking into account all locations where an animal may have been present, rather than a distribution over activity center locations only. The detection function estimated as part of an SCR model provides information about how far from its activity center an animal may move. This can be easily integrated with the estimated activity center density to give an estimated space use density surface. The resulting surface effectively smooths the activity surface density, with the amount of smoothing determined by the distances that animals move, as given by the detection function. As it is based on activity center locations, the space use density surface also depends on where traps are located and on survey effort. However, it depends less heavily on these factors than the activity center surface because the detection function does not depend on them. In particular, the space use density surface quickly stops becoming increasingly "peaked" as more survey occasions are added.

Ultimately, the appropriate density surface to use depends on the aims of the researcher. We have argued that the estimated activity center density surface should not be used as a species distribution model, because of the strong dependence on trap location and survey effort. But if the goal is to identify the activity centers of *some* animals currently in the study region (and it does not matter which ones) then it may well be an efficient way of locating these, particularly at the center of the array. If the goal is to actually *find* an animal in the study region, then it is less important where animals have their activity centers and more important to know where they spend their time, and the space use density surface is most useful. If the goal is to estimate where animals (not just the ones in the current realisation) are likely to have activity centers, then this is a species distribution question and the mean intensity surface, with intensity a function of covariates, should be used.

6 Conclusions

This paper demonstrates that the activity center density surface obtained from SCR – the summed distribution of estimated ranges across animals – cannot be used as a species distribution model. We illustrated this point in a number of ways, first with a binomial point process, then by using the Mona Lisa to simulate a Poisson point process, and finally using data from a real-world camera trap survey. All these examples returned the consistent message that density surfaces differ depending on trap location. This dependency is most obvious at large spatial scales, where moving a trap array is like "shining a torch" on a particular part of the study area, but is also present within the region in and around the trap array itself. Our main messages are:

1. SCR density surfaces cannot be interpreted not SDMs. This is both because the SCR surface makes inferences about one realisation of a spatial point process, whereas SDMs make inferences about the long run average of the process; and because the SCR surface depends systematically on the survey design.

2. The SCR density surface typically shows steep peaks and troughs close to the center of arrays, defaulting to close to the mean of the underlying process away from the array. A flat density away from traps reflects a lack of knowledge, and not a homogenous sprawl across which density is constant. We should expect some areas away from traps also to show substantial deviations from the process mean – it is just that we do not know which areas.

3. An SCR model that models mean activity center density as a function of environmental covariates can be interpreted as a SDM. Here the key difference is that the surface obtained from the covariate model is a statement about the mean intensity of the underlying process, and is independent of array location provided that the environmental covariate space has been sufficiently sampled.

4. The activity center density can be extended into a space use density

by the addition of animal movement. This is done by distributing the probability mass associated with each possible location of a particular activity center across the entire region in which, conditional of that location being the true one, an animal might be detected. The extent of this region is given by the estimated detection function parameters.

Some concluding comments...