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That's not the Mona Lisa! How to interpret spatial capture-recapture density surface estimates

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SUMMARY: Spatial capture-recapture (SCR) methods are often used to estimate density surfaces, and these are often misinterpreted. In particular, trend in density is confused with trend in uncertainty. We illustrate correct and incorrect inference visually by treating an image of the Mona Lisa as an animal activity centre (AC) intensity and simulating SCR surveys from it. We also illustrate with a real SCR survey. Inferences can be drawn about the AC intensity, the realised AC density, and the realised usage density. The first is the intensity of a point process generating ACs, the second arises from a single realisation of the process, while the third is a combination of a realisation and usage intensity about points. We show that treating realised AC density estimates as estimates of AC intensity results in invalid and misleading ecological inferences, and that estimates of the realised surface are highly dependent on where the detectors are placed. Estimates of the expected AC density surface should be obtained by estimating the intensity of a point process model for ACs. Realised usage density is obtained similarly, but includes expected usage intensity about ACs. Practitioners should state explicitly the kind of density surface they are estimating, should be careful to draw inferences appropriate to that kind of surface, and realised AC density should not be confused with AC intensity.

KEY WORDS: Spatial capture-recapture, density surface, species distribution modelling

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1. Introduction

Spatial capture-recapture (SCR) models (**???**) are now widely used to estimate animal abundance and distribution from a variety of data types, including that from camera-traps, hair snares and dung surveys, live-captures, and acoustic detectors. These methods use the location of the detectors (e.g. traps) and the locations at which animals were detected (their spatial capture histories) to estimate animal density. The methods have two basic components: a spatial model that quantifies animal activity center (hereafter abbreviated to "AC") density at all points in the survey region, and an encounter model that quantifies the expected detection frequency or detection probability, given the AC locations and the detector locations.

SCR density estimates are often presented graphically in the form of estimated density maps, these being easy to absorb and interpret, at least on the face of it. However, there are various kinds of density maps that one can produce from SCR analyses and depending on what is presented, it is easy to misinterpret the maps. The most common form of misinterpretation is treating maps that include both spatially varying uncertainty about location and spatially varying AC density estimates as if they were maps of AC density alone. There is also a lack of clarity about whether it is AC density or space use density that is being presented.

Examples include **?**, who say that such maps effectively provide "a species distribution model, even in cases where spatial covariates of abundance are unknown or unavailable", **?**, who present a map (Figure 4) that include both spatially varying uncertainty about location and spatially varying AC density and refer to it as the "spatial distribution of snow leopards", and **?**, who present the same kind of map (Figure 2) and refer to it as the "pixel-specific lion density". Minor variations on these themes can be found in many papers, for example "spatial distribution of the Amur leopard density" (**?**), "a pixelated map showing fine-scale variation in density" (**?**),"spatial variation in the location of estimated activity centers" (**?**), "pixelated SPACECAP leopard density maps" (**?**), "pixel-specific densities of elephants" (**?**), "a pixelated density map showing relative leopard density (**?**), "spatial density estimate of common leopards" (**?**), "density estimates in home-range centers (number of jaguars per 0.226km^2)" (**?**), "spatial patterns of dhole densities" (**?**), "mean posterior density of Amur tiger" (**?**), and **?** who say "Density surface maps can be produced by discretizing the state-space and tallying the number of activity centers occurring in each pixel during each MCMC iteration".

The problems with interpretation of such maps arises because (a) there are various kinds of "density", (b) uncertainty varies spatially and this fact must be (but is often not) taken into account when interpreting estimated density surfaces from SCR surveys, and (c) there is a failure to distinguish between AC density and usage density.

We start by describing different kinds of densities involved in SCR surveys, because in any discussion of density surfaces, we need to be clear about what "density" means.

1.1 *Different kinds of density*

It is useful to distinguish between four kinds of spatial "density", two of them dealing with ACs, and two dealing with space usage. Conceptually, we have some point process that governs how many ACs there are in the survey region, and where they are. Animals then use (move through and/or send a detectable signal like sound through) the space around their ACs. ACs are governed by the point process alone; usage is governed by both the point process and the movement/propagation process about the points. With this in mind, we refer to four kinds of density as follows:

(1) **The expected AC density** at a point is the intensity of the underlying point process that models where animals' ACs are over many realizations of the process. The expected number of ACs within some region is the volume under this surface over the region.

(2) **The realised AC density** is only well defined if continuous space is partitioned into what we will call cells. The realised AC density in a cell is the actual (as opposed to expected) number of ACs per unit area within the cell (i.e., the number divided by the area of the cell) at the time of the survey. The realised ACs themselves are points in space, not densities.

(3) **The expected usage density** at a point is the expected number of animals per unit area that occur at that location at a random point in time, over many realizations of the process that generates ACs.

(4) **The realised usage density** at a point is the expected number of animals per unit area that occur at that location at a random point in time during the survey. The realised usage density at a point for one animal is the probability density of finding the animal at that location at a random time during the survey. The realised usage density surface is obtained by summing over animals.

We focus on densities 1, 2, and 4. Figure 1 shows examples of each, except that we show the realised AC locations rather than realised AC densities in sub-regions of space. Realised AC densities can only be plotted when space has been cut into cells; in continuous space the density is zero everywhere except at AC locations, where it approaches infinity.

[Figure 1 about here.]

1.2 *Estimated density surfaces*

If we are interested in explaining why density tends to be high in some places and lower in others, or in characterising the process that governs the distribution of ACs, then we are primarily interested in estimating a density surface like that shown in Figure 1(a). In this example, it is easting that influences this density, but in general it might be any of a wide variety of habitat or environmental covariates, some of which may be unobserved and evidenced only by spatial clustering of ACs.

If we are interested only in where the ACs are, and not in explaining why they are there, then Figure 1(b) suffices. But suppose that we observe ACs with some error. For example, Figure 1d-f shows the distributions of estimated AC locations when the locations in (b) are estimated with bivariate normal errors with (d) small standard errors, (e) larger standard errors, and (f) standard errors increasing linearly from the center of the plot. The estimation uncertainty “spreads” each AC according to a bivariate normal distribution, with greater spreading when there is greater uncertainty.

Ignoring the actual AC dots (because they cannot be observed), Figure 1(d) gives a reasonable visual representation of where the ACs are. It is much more difficult to pick out individual ACs from Figure 1(e), but it gives a reasonable representation of where the high- and low-density regions of ACs are – much like Figure 1(a), but customised somewhat for this particular realisation of AC locations rather than their long-run average locations. Note, however, that these two figures are representations of exactly the same set of ACs and that if one interprets them as plots of AC density, they contradict each other. Figure 1(d) says that almost all the region has low density (red in the plot) and that there are lots of small high-density regions, while Figure 1(e) says that there is much less variation in density, that there are large swathes of higher density (the yellow towards the right) and large swathes of low density towards the left. The reason why Figure 1(e) shows less variation in density is not that there is less variation in the population (there are exactly the same ACs in both (d) and (e)), it is that we are less sure about the location of the ACs in (b). To interpret this as less variation in AC density is to invite incorrect ecological inferences.

Now what about Figure 1(f)? If this is interpreted as indicating where the high and low-density regions are, it is misleading. It says that the highest density region is in the center of the plot, and that the region with most variation in density is the central region, which is not true.

The fact that there is only small observation error in the center of the plot and large observation error at the edges means that the ACs near the center are not spread much and therefore appear as higher peaks in the surface, with low regions where there are no ACs. Near the edges of the plot, on the other hand, observation error is high and ACs are spread a lot, which both flattens the peaks at individual AC locations and "fills in" the troughs where there are no ACs.

It is a feature of SCR surveys that the AC locations of individuals farther from the detector array tend to be estimated with greater uncertainty than individuals within the array. This is illustrated in Figure 2, which shows the estimated probability density functions for ACs of two animals detected on a simulated SCR survey with a 4×4 array placed in the center of the population shown in Figure 1(b). The reason contours in the top right of the figure "avoid" the triangle is because the detection function range, estimated from the whole survey, not just the points shown, is large and if the AC was near the triangle, other detectors would have high probability of detecting it. The fact that they did not makes them "repel" the AC.

[Figure 2 about here.]

2. SCR density estimation methods

Maximum likelihood (ML) and Bayesian SCR estimation methods are documented in a good number of papers, starting with **?** and **?**. Both ML and Bayesian inference are based on SCR likelihood functions that include a component specifying the AC density surface, which may depend on spatially-referenced covariates (the linear density surface shown in Figure 1(a) is an example). The density surface is typically of the form $D(\boldsymbol{s}) = \exp\left\{\beta_0 + \sum_{k=1}^{K} \beta_k x_k(\boldsymbol{s})\right\}$, where $\boldsymbol{s}$ is a point in the plane, $x_k(\boldsymbol{s})$ is the kth of K spatially-referenced covariates, evaluated at $\boldsymbol{s}$, β_0 is an intercept parameter, and β_k is the slope parameter for the kth spatially-referenced covariate. ML and Bayesian methods are able to estimate $\beta_0, \ldots, \beta_K$, and hence estimate the expected AC density surface.

Given spatial capture histories, ML and Bayesian methods are also able to estimate the locations of ACs (like those shown in Figure 1(b), for example). While ACs are points, there is always uncertainty associated with estimating their locations, so that SCR estimates of AC locations are probability density functions (PDFs), not points. Estimates of these PDFs are conditional on the spatial capture histories of the individuals concerned – because the capture histories contain the information on where each animal's AC was (see the capture histories and estimated location densities in Figure 2, for example). Details of how one obtains these estimated AC PDFs are contained in Section 4.3 of **?** for ML methods and the section "Estimating derived parameters" on page 3238 of **?** for Bayesian methods.

Note that we can obtain AC PDFs for undetected animals, because although the animals were unobserved, we know their capture histories – namely no capture at every detector. Note also that all undetected animals will have the same AC PDF because they all have the same capture history (unless there are individual-level covariates that affect detection probability estimates, a complication that we ignore here in order to present as clear and uncomplicated an exposition of they key points of this paper as we can).

Suppose that we estimate from an SCR survey that there are $\hat{N}$ animals within the survey region. If one adds up the AC PDFs for all n detected animals, and the $\hat{N} - n$ AC PDFs of the undetected animals, at all points in the survey region, one gets a surface that is in many publications (including those listed in the Introduction) interpreted as a density surface for ACs, or sometimes for animal locations. This is an estimate of the realised AC density. It has been referred to as the estimated distribution, or density of *animals*. However, animals distribute themselves around their ACs, so that AC density and animal density are not the same thing. Suppose for example, that we are certain that there is exactly one AC in a region that has surface area 1 (so that AC density in this region is 1). Suppose also that the animal with an AC in this region ranges wider than this region, and spends exactly half its time in this region. It is not certain that there is an animal in the region at any time, so that animal density will be less than 1. In this example, it would be fair to say that the *animal* density in the region is 0.5. To avoid confusion, we refer to this as the "usage density" rather than "animal density". Details of how one estimates the realised usage density surface from an estimate of the realised AC density surface are given in Supplementary Material B.

In summary, there are three kinds of estimated surface of interest here:

- An estimate of the expected AC density surface: This is an estimate of the density model component of the SCR model, which governs the number and locations of ACs.
- An estimate of the realised AC density surface: This is the combined estimates of realised AC densities of all animals, conditional on each animal's capture history.
- An estimate of the realised usage density surface: This is the combined space usage density of animals, conditional on each animal's capture history.

3. Methods

We illustrate what each of the estimated surface gives the practitioner, and what interpretations of the surfaces are valid and useful, by simulating data from a density surface that has an easy visual interpretation. To do this, we turned to one of the most recognisable images in Western culture, the Mona Lisa, into a density surface. We created a 50×50 pixel greyscale version of a region of the original image (Figure 3a) in which greyscale values give the true density of ACs, and lighter areas correspond to higher densities.

The image's pixel intensities can be arbitrarily scaled to a constant sum corresponding to the expected number of activity centers over the surface. We chose this sum to be 80, on the basis that this is sufficient to illustrate our main points and also broadly typical of many wildlife surveys. We then generated a single realisation of points from this surface (a Poisson distribution with mean 80), which resulted in 85 ACs being generated (Figure 3b).

[Figure 3 about here.]

We simulated capture histories from this population using a half-normal encounter rate function with the spatial scale parameter $\sigma = 4$ and two different detector arrays: a 3×3 array centred at $x = 18$ and $y = 24$ (Figure 4), and a 7×7 array covering the entire image (Figure 5). Both arrays had a regular spacing of $2\sigma = 8$ between detectors. Simulated capture histories were Poisson random variables with expected values equal to the encounter rate function evaluated at the distances of detectors from ACs. In order to illustrate how realised and expected AC density surfaces change with increasing sample sizes, we simulated capture histories with three different survey effort levels, obtained by varying λ_0 so that the average number of detections per detected individual was approximately two, four, or eight (corresponding to $\lambda_0 = 1.8, 5.2$, and 11.1 for the 3×3 grid, and $\lambda_0 = 0.7, 2.5$, and 5.5 for the 7×7 grid). This generated between 47 and 318 detections of between 23 and 39 individuals for the 3×3 grid (Figure 4), and between 94 and 702 detections of between 54 and 85 individuals for the 7×7 grid (Figure 5).

To estimate the realised AC surface, we assumed a model with constant density. To estimate an expected density surface, we generated a covariate by blurring the true density surface (Figure **??**). Pixel intensities were rescaled after blurring so that the number of expected activity centers remained the same as in the original surface (i.e., 80). Because it is based on true density the covariate is informative about the true densities, although the strength of the association is diluted by the blurring. We estimated an expected AC density surface assuming a model in which density is a function of covariate values. Note that, because density is parameterised with a log link (see Section 2) but the blurred surface is obtained directly from the true density surface (so that $D(\mathbf{s}) \approx x_k(\mathbf{s})$, with the degree of blurring determining the accuracy of approximation), covariate values were log-transformed to ensure the model was correctly specified.

Most of the examples of unclear or incorrect interepreations of density surfaces that we listed in the introduction are made in the context of Bayesian methods. To show that correct interpretations do not depend on the inferential method used, models were estimated using both maximum likelihood inference (using the `secr` package (?)) and Bayesian inference (using the `NIMBLE` package (??)) in R version 4.1.2. We report the maximum likelihood estimates here; the Bayesian estimates are not materially different and are reported in Supplementary Material A.

3.1 *Results*

A striking feature of realised AC density surface estimates shown in Figure 4 (top row) are they do not recover the Mona Lisa in any recognisable way. They are not designed to do so. The Mona Lisa image is an expected density surface, with the value of the surface at any point giving the intensity of the point process generating ACs at that point. Realised AC density surfaces estimate the number of ACs in each cell *in this realisation of that point process*, given our observed data. In the vicinity of the array this provides information about the location of ACs for individuals detected during the survey, with the resolution of the habitat mask providing an upper bound on the precision with which locations can be estimated.

Away from the array the surface is flat because individuals with ACs far from the array are not detected, there is no information in the sample on their location other than that contained in the SCR estimate of mean density, and so all the model "knows" about AC location far from the array is that they occur in space at the estimated mean density of ACs.

The highest values of the realised AC density surface tend to be in the interior of the array, not because more ACs are expected to be there, but because animals with ACs inside the array tend to be detected more often and across more detectors than animals on the periphery, which allows their AC locations to be estimated more precisely. For the same reasons, increasing survey effort does not improve the resemblance to the Mona Lisa – the realised AC density surface just becomes more "spiked" overall, with highest densities continuing to lie within the array.

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 (Figure 4, bottom row). Recovery may not be this good in reality – we simulated our covariate to be related to true density – and extrapolation so far beyond the area where data was collected is in any case ill-advised. Notwithstanding this, it is true in general that because the expected AC surface depends on the relationship between the covariate and density, the model uses estimates of this relationship obtained where it has lots of information (within the array) to infer density beyond the array.

Importantly, the estimates within the dashed rectangle are almost identical for all array placements - these estimates are not sensitive to where the array is placed.

[Figure 4 about here.]

[Figure 5 about here.]

4. Discussion

The realised AC 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. A species distribution model will tend to place higher densities at locations where environmental covariates are most favourable for the species, and spatial variation in the density surface will depend on how environmental covariates change across space and the strength of the relationship between the covariates and species density.

In contrast, high realised AC density occurs where the model is most certain that an activity center is located. Crucially, location of high- and low-density regions of a realised AC density surface depends on (a) where detectors are 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 where the array was placed), and (b) on survey effort (with higher effort resulting in higher troughs and spikes in the realised AC density surface). Different arrays produce quite different estimates for exactly the same AC locations. A useful metaphor here is of SCR as a torch shining a light onto the true activity centers – what you see depends on where you shine the torch (detector locations) and how brightly you shine it (survey effort). If you interpret the uniform darkness outside of the beam to mean that everything outside the beam is the same, you fundamentally misunderstand the nature of torches and will draw fundamentally incorrect conclusions.

Realised AC surfaces tend to be flat away from where detectors are located. It is important to understand that this flatness reflects a lack of knowledge about the density surface away from detectors, and does not mean that the density surface is flat away from detectors. This point is clearly stated in **?**, who say (p165-166) "As we move away from 'where the data live' (away from the detector array) we see that the density approaches the mean density. This is a property of the estimator as long as the detection function decreases sufficiently rapidly as a function of distance. ... predictions tend toward the global mean as the influence of data diminishes", but is misinterpreted whenever researchers explicitly or implicitly treat realised activity center densities as maps of the spatial distribution of activity centers across the study area.

Another way to see that flatness away from detectors reflects uncertainty rather than homogenous density is to plot lower and upper percentiles at each pixel, rather than just the posterior mean – the differences between these percentiles would be large away from detectors and small close to detectors. It seems that this is rarely done, or at least reported in the literature; a practice that would be worth changing.

When considering realised ACs, 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 detectors are located - because the capture history depends on where the detectors are located. This is the case regardless of whether one works in a Bayesian or frequentist framework. The same is true of the realised AC 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 detector 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 the answer to the question for them is really just "nowhere near where detectors are located".

None of this precludes realised AC density 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 detectors are located. Realised AC densities 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 detectors; 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. They also cannot answer questions like "are animals clustered in space?" or "is animal density heterogeneous?" because the realised density surface will always exhibit variability, even if animal densities are truly a realisation of a homogeneous Poisson point process.

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 environmental 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 detectors cover a sufficient range of covariate values to estimate that relationship well. The resulting surfaces are no longer strongly tied to one particular realisation of the Poisson process. Rather, they show the (estimated) intensity of the underlying process assumed to generate activity centers. These expected densities will be highest where environmental covariates are most favourable (such as further south in Figure **??**). They answer the questions "Where are the high- and low-density regions?" and "What spatial variables are good predictors of the high- and low-density regions?" in a way that is consistent with how this question is answered by species distribution models.

Using covariate models, and associated model-based inference, is not without issues – there is a danger of extrapolating the density surface beyond the range of covariates around the detectors, and the relationship with density and covariate is assumed to be the same everywhere as it is around the detectors. The extent to which the expected activity center surface predicts where animals have their activity centers *in this realization of the process* depends on the strength of the covariate relationship and on the number of activity centers, each of which is assumed to be an independent draw from the underlying process.

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 or encounter 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 realised AC density to give an estimated realised *usage* density surface. The resulting surface effectively smooths the realised AC density surface, with the amount of smoothing determined by the distances that animals move. As it is based on realised AC density, the usage density surface also depends on where detectors are located and on survey effort. However, it depends less heavily on these factors than the realised AC surface because the detection function or encounter function does not depend on them. In particular, the realised usage density surface quickly stops becoming increasingly "peaked" as survey effort increases.

We constructed individual usage distributions using the encounter function from our SCR model, but this may not always be appropriate. For example, if individuals cannot fully explore their home range within the duration of the survey, then we would not expect the spatial range of the detection function to match the extent of an animal's usage distribution. Even for longer surveys, it may not be sensible to relate the range of the encounter function to the size of the region used by an individual even for longer surveys, so care should be taken when this practice is used. For example, **?** found that the spatial scale of the encounter rate function for brown bears (*Ursus arctos*) estimated using SCR was not consistent with spatial usage parameters estimated from other data sources, although **?** did not detect any such inconsistency for a population of fishers (*Pekania pennanti*). If alternative data sources are available (e.g., telemetry, or opportunistic data such as hair or scat samples) they may be incoprorated for improved estimation of individual usage distributions (**?**). Our method also assumes that home ranges are circular, however their shapes are likely to be modified by variables relating to population and landscape connectivity (see **?**, for a review).

Ultimately, the appropriate density surface to use depends on the aims of the researcher. We have argued that the estimated realised activity center density surface should not be used as a species distribution model, because of the strong dependence on detector 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 realised usage 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 expected AC surface, with density a function of covariates, should be used.

5. Conclusions

Our main messages are:

(1) Realised activity center density surfaces cannot be interpreted as SDMs. This is both because these surfaces draw inferences about one realisation of a spatial point process, whereas SDMs make inferences about the long run average of the process; and because the surface depends systematically on where detectors are located.

(2) The realised activity center density surface typically shows highest peaks and deepest 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 detectors reflects a lack of knowledge, and not constant density. We should expect that in reality some areas away from detectors have 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 – what we call an expected activity center surface – 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) Realised activity center densities can be extended into realised usage densities. This is done by using the estimated encounter rate function to "spread" animals about their estimated ACs according to the expected number of encounters of the animal as distance from its AC increases.

Acknowledgements

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Data availability

All data and code used in the paper, along with model objects and results, are available at `https://github.com/david-borchers/monalisa`. If accepted we would use Zenodo to create a permanent DOI link to the version of the repository used to generate the results in the paper.

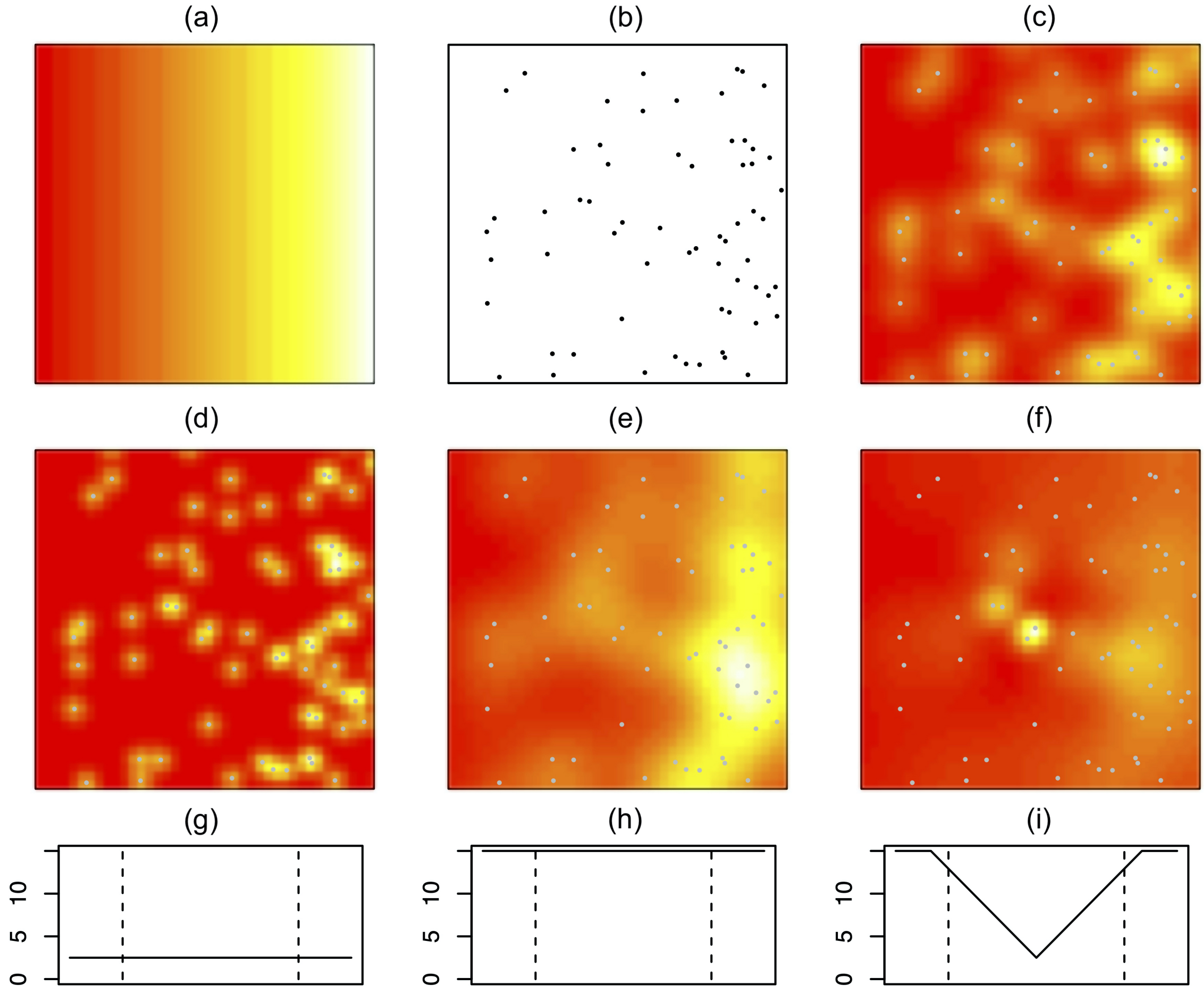

Figure 1. Examples of (a) an expected AC density surface, (b) a realisation of ACs from this density surface, and (c) the associated realised usage density surface (with ACs shown as grey dots). Panels (d) to (f) show the realised density of the ACs in (b), when observed with bivariate normal estimation errors with standard errors (d) $\sigma = 2.5$, (e) $\sigma = 15$, and (f) $\sigma = 2.5$ at the center of the plot, rising linearly to $\sigma = 2.5$ by the edge of the plot. True ACs shown as grey dots. The colour scales of panels (d) to (f) are such that the highest and lowest densities in each plot is the same. Panels (g) to (i) plot the standard errors of the observation errors against the x-axis. Vertical dashed lines show the extent of the survey region in panels (d) to (f); a buffer beyond this is included because spreading of points outside it affect the plot within the survey region. Color version of figures can be found in the electronic version of this article.

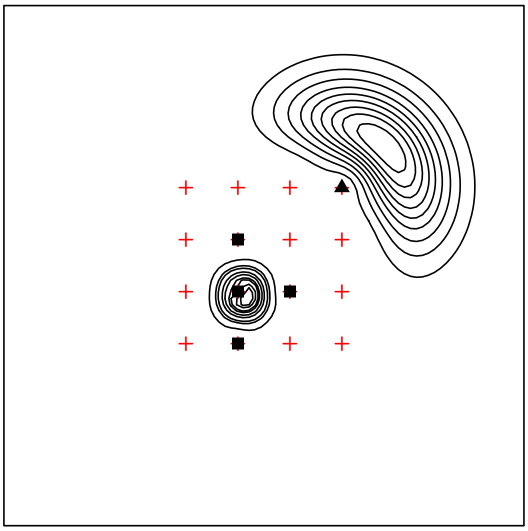

Figure 2. Estimated probability density function contours for two detections in an SCR survey of the population shown in Figure 1(b). Detectors are shown as red crosses. The lower left individual was detected at detectors indicated by black squares, the upper right individual only by the top right detector indicated by a black triangle.

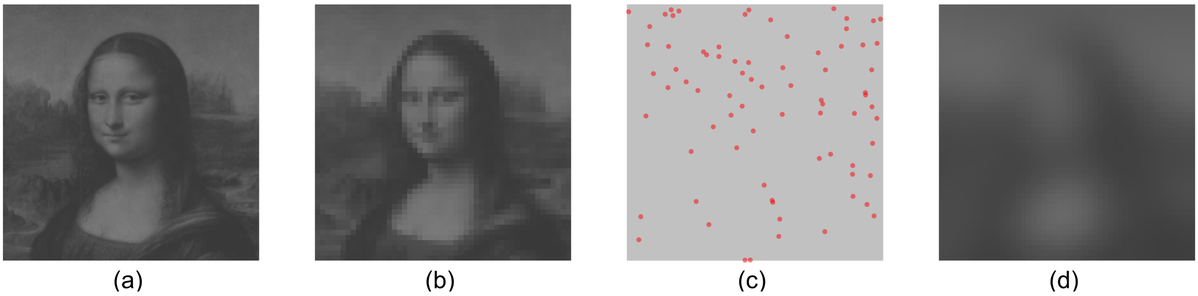

Figure 3. Input data for the Mona Lisa simulation study. Panel (a) shows a greyscale version of the Mona Lisa treated as an expected AC density surface, (b) a single realisation of 85 ACs generated from the density surface in (a), (c) a spatially-varying covariate used to estimate expected AC density surfaces.

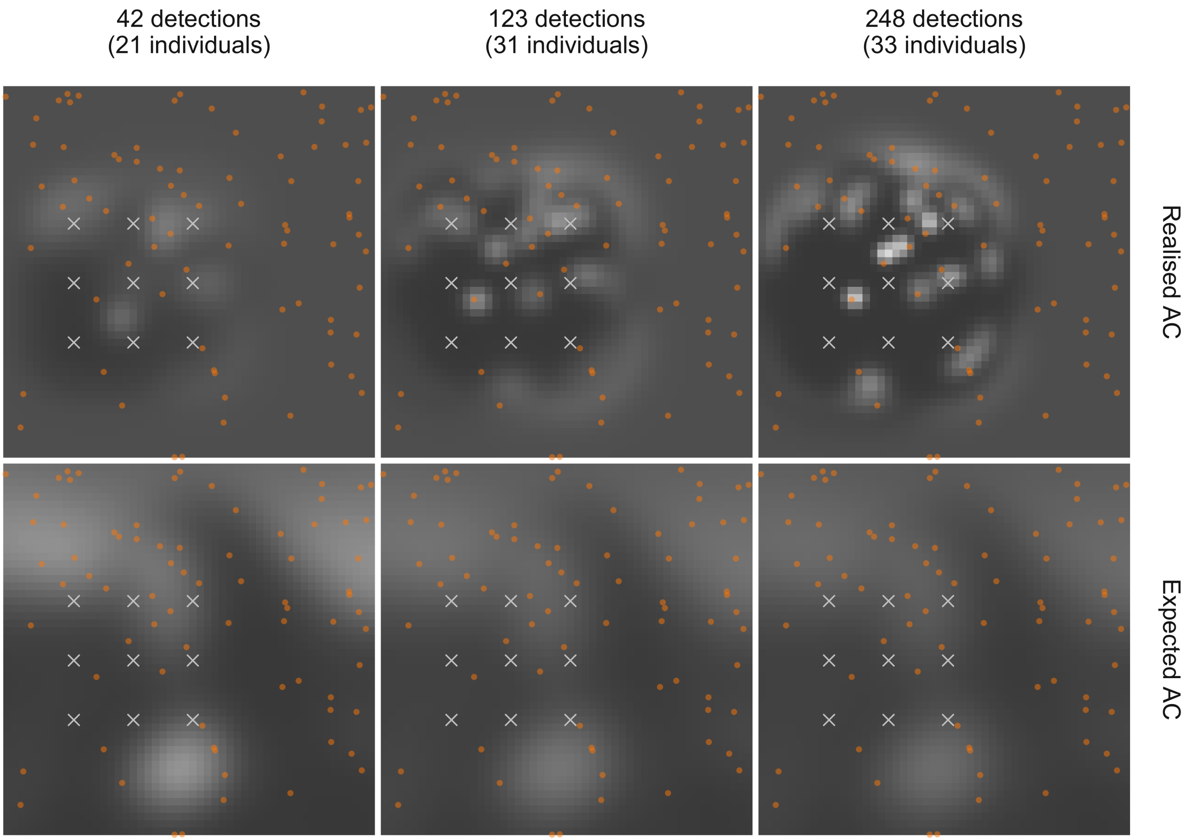

Figure 4. Plots (a), (b), (c) show estimated realised AC surfaces estimated using the 3×3 array indicated by grey crosses under three levels of survey effort. True AC locations are shown as orange dots. Plots (d), (e), (f) show expected activity center surfaces estimated using a model in which density is a function of a simulated spatially-varying covariate (see Figure **??**).

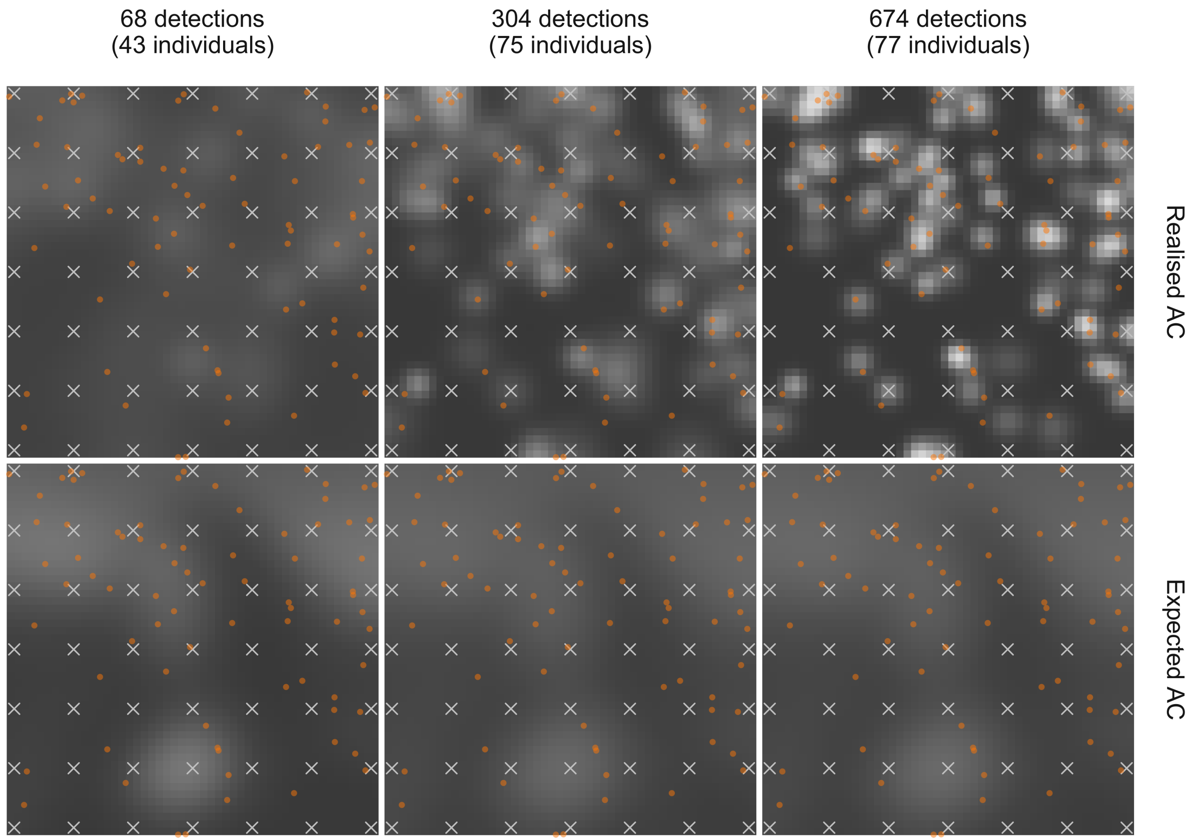

Figure 5. Plots (a), (b), (c) show estimated realised AC surfaces estimated using the 7×7 array indicated by grey crosses under three levels of survey effort. True AC locations are shown as orange dots. Plots (d), (e), (f) show expected activity center surfaces estimated using a model in which density is a function of a simulated spatially-varying covariate (see Figure **??**).