

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

4 David L. Borchers^{1,*}, Ian Durbach¹, Rishika Chopara², Ben C.
5 Stevenson², Rachel Phillip¹, and Koustubh Sharma³

6 ¹Centre for Research into Ecological and Environmental Modelling,
7 School of Mathematics and Statistics, Univeristy of St Andrews,
8 The Observatory, St Andrews, Fife, KY16 9LZ, Scotland

9 ²Department of Statistics, University of Auckland, Auckland 1010,
10 New Zealand

11 ³Snow Leopard Trust, Seattle, Washington, United States of
12 America

13 *Corresponding author: dlb@st-andrews.AC.uk

14 **1 Summary**

15 1. Non-uniform denisty surfaces obtained from spatial capture-recapture (SCR)
16 analyses are often misinterpreted and this leads to incorrect inferences
17 about the populations under study. Spatial variation in the surface of
18 interest is often counfused with spatial variation in the amount of infor-
19 mation in the sample about the surface of interest. There is also often a
20 lack of clarity about what the surface of interest really is.

- 21 2. We focus on three distinct kinds of surface: (1) the expected activity
22 centre (AC) density surface, (2) the realised AC density surface, and (3)
23 the realised usage density surface. The first of these estimates the intensity
24 of the point process generating ACs, the second estimates the AC locations
25 from a realisation of the process, the third estimates the expected space
26 usage from a realisation of the process. For easy visual interpretation, we
27 use a monochrome image of the Mona Lisa as the true AC density surface
28 and illustrate correct and incorrect inferences from simulated SCR surveys
29 with this density. We also illustrate with a real SCR survey of tigers in
30 the Nagarahole game reserve.

- 31 3. We show that treating estimates of the realised AC density surface as a
32 species distribution map or an estimate of the expected AC density sur-
33 face results in invalid and misleading ecological inferences. This surface
34 is highly dependent on where the detectors are placed and very differ-
35 ent surfaces can be obtained by surveying exactly the same animals with
36 detectors placed at different locations. A valid way to obtain a species
37 distribution map or an estimate of the expected AC density surface from
38 SCR data is to estimate the intensity of a point process model for ACs,
39 which may depend on spatially-referenced covariates. Realised usage den-
40 sity surfaces are obtained similarly, but include expected movement about
41 ACs.

- 42 4. To avoid misinterpretation, practitioners should state explicitly the kind
43 of density surface they are estimating and should be careful to draw in-
44 ferences appropriate to that kind of surface. In particular, realised AC
45 density surfaces should not be interpreted as if they were expected AC
46 density surfaces.

47 **Keywords:** Spatial capture-recapture, density surface

2 Introduction

Spatial capture-recapture (SCR) models (Efford, 2004; Borchers & Efford, 2008; Royle & Young, 2008) 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, 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 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 map 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, but there is also a lack of clarity about whether it is AC density or space use density that is being presented.

Examples include Dorazio & Karanth (2017) which says that such maps effectively provide “a species distribution model, even in cases where spatial covariates of abundance are unknown or unavailable”, Alexander, Gopalaswamy, Shi & Riordan (2015), which presents a map (Figure 4) that include both spatially varying uncertainty about location and spatially varying AC density and refers to it as the “spatial distribution of snow leopards”, and Elliot & Gopalaswamy (2016), which presents the same kind of map (Figure 2) and refers to it as the “pixel-specific lion density”.

The problems with interpretation of such maps arises because (a) there are

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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) 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.

2.1 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 (abbreviating “activity centre” to “AC”):

1. **The expected AC density** at a point is the intensity of the underlying point process that models where animals’ ACs are “on average” i.e. 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** in a region is the expected number of visits per unit area of animals to the area, averaged over all possible AC

locations, over the course of a survey (it is the expected number of visits divided by the area).

4. **The realised usage density** in a region is the expected number of animal visits per unit area to the area over the duration of the survey (the expected number of visits divided by the area), *conditional* on the AC locations.

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.

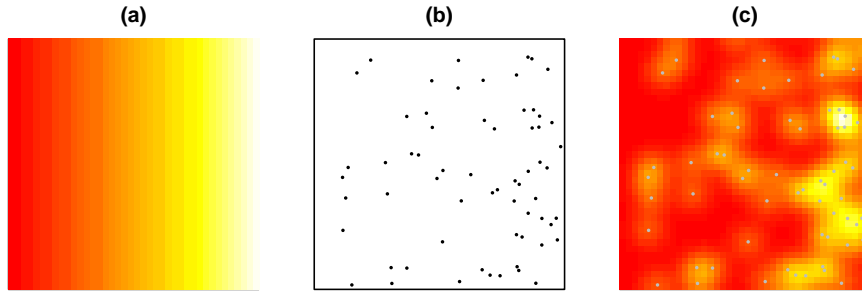


Figure 1: Examples of (a) an expected AC density surface, (b) a realisation of ACs from this density surface, and (c) the associated realised usage density surface (with ACs shown as grey dots).

2.2 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.

123 If we are interested only in where the ACs are, and not in explaining why they
 124 are there, then Figure 1(b) suffices. But suppose that we observe ACs with some
 125 error. For example, Figure 2 shows the distributions of estimated AC locations
 126 when the locations are estimated with bivariate normal errors with (a) small
 127 standard errors, (b) larger standard errors, and (c) standard errors increasing
 128 linearly from the centre of the plot. The estimation uncertainty “spreads” each
 129 AC according to a bivariate normal distribution, with greater spreading when
 130 there is greater uncertainty.

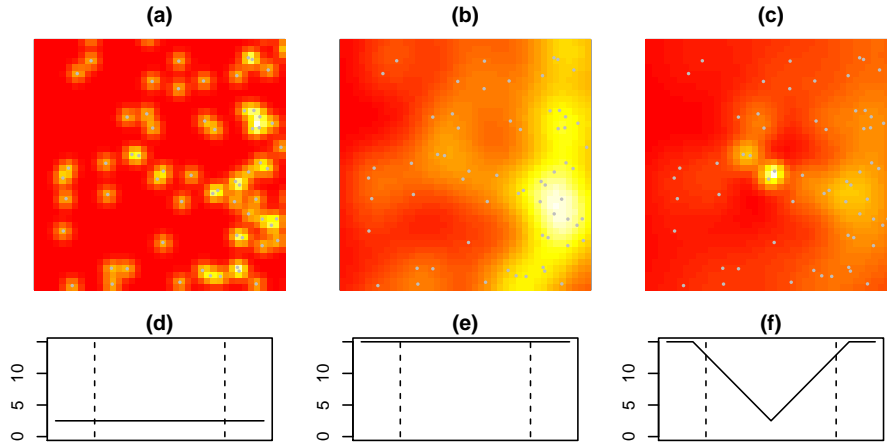


Figure 2: Examples of the density of the ACs of Figure 1(b), when observed with bivariate normal estimation errors with standard errors (a) $\sigma = 2.5$, (b) $\sigma = 15$, and (c) $\sigma = 2.5$ at the centre of the plot, rising linearly to $\sigma = 2.5$ by the edge of the plot. True ACs shown as grey dots. The colour scales of panels (a) to (c) are such that the highest and lowest densities in each plot is the same. Panels (d) to (f) plot the standard errors of the observation errors against the x-axis. Vertical dashed lines show the extent of the survey region in panels (a) to (c); a buffer beyond this is included because spreading of points outside it affect the plot within the survey region.

131 Ignoring the actual AC dots (because they cannot be observed), Figure 2(a)
 132 gives a reasonable visual representation of where the ACs are. It is much more
 133 difficult to pick out individual ACs from Figure 2(b), but it gives a reasonable
 134 representation of where the high- and low-density regions of ACs are – much
 135 like Figure 1(a), but customised somewhat for this particular realisation of AC
 136 locations rather than their long-run average locations. Note, however, that these

137 two figures are representations of exactly the same set of ACs and that if one
138 interprets them as plots of AC density, they contradict each other. Figure 2(a)
139 says that almost all the region has low density (red in the plot) and that there
140 are lots of small high-density regions, while Figure 2(b) says that there is much
141 less variation in density, that there are large swathes of higher density (the
142 yellow towards the right) and large swathes of low density towards the left. The
143 reason that Figure 2(b) shows less variation in density is not that there is less
144 variation in the population (there are exactly the same ACs in both (a) and (b)),
145 it is that we are less sure about the location of the ACs in (b). To interpret this
146 as less variation in AC density is to invite incorrect ecological inferences.

147 Now what about Figure 2(c)? If this is interpreted as indicating where the
148 high and low-density regions are, it is misleading. It says that the highest density
149 region is in the centre of the plot, and that the region with most variation in
150 density is the central region, which is not true.

151 The fact that there is only small observation error in the centre of the plot
152 and large observation error at the edges means that the ACs near the centre
153 are not spread much and therefore appear as higher peaks in the surface, with
154 low regions where there are no ACs. Near the edges of the plot, on the other
155 hand, observation error is high and ACs are spread a lot, which both flattens
156 the peaks at individual AC locations and “fills in” the troughs where there are no
157 ACs. We see the same effect with the usage density maps (Figure 3), but less
158 pronounced because the usage about the ACs already “spreads” around points
159 before any observation error occurs.

160 It is a feature of SCR surveys that the locations of individuals farther from
161 the detector array tend to be estimated with greater uncertainty than individ-
162 uals within the array. This is illustrated in Figure 4, which shows the esti-
163 mated probability density functions for two animals detected on a simulated
164 SCR survey with a 4×4 array placed in the centre of the population shown in
165 Figure 1(b). (The reason contours top right “avoid” the triangle is because the
166 detection function range, estimated from the whole survey, not just the points

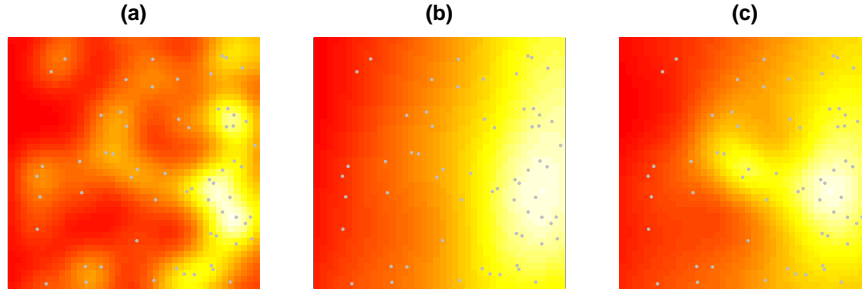


Figure 3: Examples of the usage density of Figure 1(c), when observed with bivariate normal estimation errors with standard errors (a) $\sigma = 2.5$, (b) $\sigma = 15$, and (c) $\sigma = 2.5$ at the centre of the plot, rising linearly to $\sigma = 2.5$ by the edge of the plot. True ACs shown as grey dots. The colour scales of the three plots are such that the highest and lowest densities in each plot is the same.

167 shown, is large and if the AC was near the triangle, other detectors would have
 168 high probability of detecting it. The fact that they did not makes them “repel”
 169 the AC.)

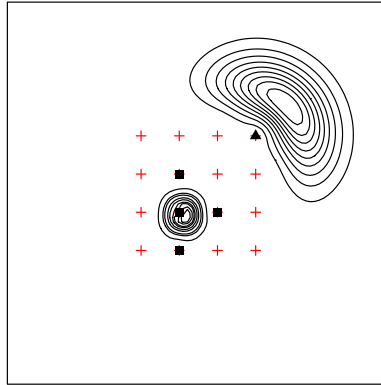


Figure 4: Estimated probability density function contours for two detections of an SCR survey of the population shown in Figure 1(b). Detectors are shown as red crosses. The lower left individual was detected at detectors indicated by black squares, the upper right individual only by the top right detector indicated by a black triangle.

3 SCR density estimation methods

Maximum likelihood (ML) and Bayesian SCR estimation methods are documented in a good number of papers, starting with Borchers & Efford (2008) and Royle & Young (2008), and we do not repeat the details here. 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 $D(\mathbf{s}) = \exp \left\{ \beta_0 + \sum_{k=1}^K \beta_k x_k(\mathbf{s}) \right\}$, where \mathbf{s} is a point in the plane, $x_k(\mathbf{s})$ is the k th of K spatially-referenced covariates, evaluated at \mathbf{s} , β_0 is an intercept parameter, and β_k is the slope parameter for the k th spatially-referenced covariate. ML and Bayesian methods are able to estimate β_0, \dots, β_K , and hence to estimate the expected AC density surface.

Given spatial capture histories, ML and Bayesian methods are also able to estimate the locations of ACs. (Locations 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 4, for example). Details of how one obtains these estimated AC PDFs are contained in Section 4.3 of Borchers & Efford (2008) for ML methods and the section “Estimating derived parameters” on page 3238 of Royle, Karanth, Gopalaswamy & Kumar (2009) 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 PDF¹ because they all have the same capture history.

¹This is not the case if there are individual-level covariates that affect detection probability estimates, but this is a complication that we ignore here in order to present as clear and uncomplicated an exposition of the key points of this paper as we can.

198 Suppose that we estimate from an SCR survey that there are \hat{N} animals
 199 within the survey region. If one adds up the AC PDFs for all n detected
 200 animals, and the $\hat{N} - n$ AC PDFs of the undetected animals, at all points in the
 201 survey region, one gets a surface that is in many publications (including those
 202 listed in the Introduction) interpreted as a density surface for ACs, or sometimes
 203 for animal locations. This is an estimate of the realised AC density.

204 It has been referred to as the estimated distribution, or density of *animals*.
 205 However, animals distribute themselves around their ACs, so that AC density
 206 and animal density are not the same thing. Suppose for example, that we are
 207 certain that there is exactly one AC in a region that has surface area 1 (so that
 208 AC density in this region is 1). Suppose also that the animal with AC in this
 209 region ranges wider than this region, and spends exactly half its time in this
 210 region. It is not certain that there is an animal in the region at any time, so
 211 that animal density will be less than 1. In this example, it would be fair to say
 212 that the *animal* density in the region is 0.5. To avoid confusion, we refer to
 213 this as the “usage density” rather than “animal density”. Details of how one
 214 estimates the realised usage density surface from an estimate of the realised AC
 215 density surface are given in Appendix A.

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

- 217 • An estimate of the expected AC density surface: This is an estimate of the
 218 density model component of the SCR model, which governs the number
 219 and locations of ACs.
- 220 • An estimate of the realised AC density surface: This is the combined esti-
 221 mates of realised AC densities of all animals, conditional on each animal's
 222 capture history.
- 223 • An estimate of the realised usage density surface: This is the combined
 224 space usage density of animals, conditional on each animal's capture his-
 225 tory.

4 Methods

We illustrate what each of the three kinds of estimated surface gives the practitioner, and what interpretations of the surfaces are valid and useful, by (a) simulating data from a density surface that has easy visual interpretation, and (b) using the Ngarahole SCR tiger survey data kindly provided by the first author of Dorazio & Karanth (2017).

4.1 Reproducing the Mona Lisa

For easy visual interpretation, we turned one of the most recognisable images in Western culture, the Mona Lisa, into a density surface. We created a greyscale version of a region of the original image (Figure 5, “True Density”) in which greyscale values give the true density of ACs, and lighter areas correspond to higher densities.

We then used the density surface 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 7,500, resulting in 7,451 ACs being generated, which we plot in Figure 5, “Realisation 1” as a density at 50×50 pixel resolution. This realisation has the advantage of closely reproducing the source image, and when we conduct SCR surveys with this population, it gives us an indication of the asymptotic behaviour of SCR density estimators, i.e. as sample size gets very large. We also generated a much smaller second realisation of 84 points (Figure 5, “Realisation 2”). This realisation captures the Mona Lisa only at an extremely gross level (the darkest region corresponding to the hair can be picked out if you squint at the image long enough!), but is a useful aid to understanding some properties of the estimators.

We simulated SCR surveys of the population, using a variety of detector arrays and also varying sample size. Different arrays and detection functions were used for the large and small populations described above. With the large number of activity centers (“Realisation 1” in Figure 5), we used a 3×4 array

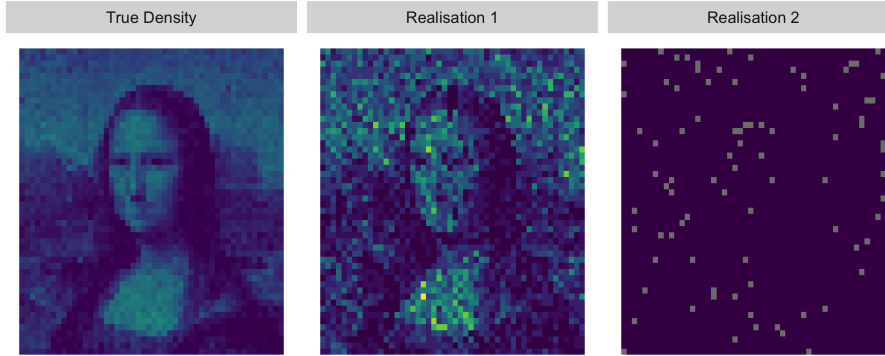


Figure 5: Input data for the Mona Lisa simulation study. A grayscale version of the Mona Lisa (“True Density”) is treated as an expected AC density surface, from which we generated a sample of 7,451 and 84 ACs and plotted these as realised AC density surfaces at 50×50 pixel resolution (“Realisation 1” and “Realisation 2”, respectively).

placed at four different locations (Figure 6). These have an average spacing of $4 = 2\sigma$ between detectors. We simulated capture histories using a half-normal detection function with g_0 , the probability of detection at a single detector placed at an AC, set to 0.5, and σ , the spatial scale parameter, set to 2. In order to investigate the asymptotic behaviour of the realised and expected AC density surfaces, we simulated very large samples from each array: the mean number of animals detected on a single survey was 1,150 and the mean number of detections was 11,304 (i.e. an average of about 10 detections per animal).

When using relatively few activity centers (“Realisation 2” in Figure 5), 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 3×3 array with an average spacing of 8 between detectors, double that used previously. We used two different locations of the detector array and simulated capture histories with three different survey effort levels, generating between 79 and 526 detections of between 31 and 44 individuals (see Figure 8). After simulating capture histories for these arrays, we estimated the realised

and expected AC surfaces for each simulation.

To estimate the realised AC surface, we assumed a model with constant density. To estimate an expected density surface, we generated covariates by manipulating the image to blur it, using two levels of blurring, as shown in Figure 8, with “Strong” corresponding to a strong covariate effect (relatively little blurring) and “Moderate” corresponding to a weaker covariate effect (more blurring). Because they are based on true density, these covariates are very informative about the true densities although the strength of the association between the covariate and true density is substantially lower for the “Moderate” covariate. For each of these covariates we estimated a corresponding expected AC density.

We simulated capture histories and from them estimated the realised AC density surface and the realised usage density surface for each simulation and compared them to the true population density surface. We conducted maximum likelihood inference using the *secr* package in R version 3.4.3 and Bayesian inference using the NIMBLE package, also in R. Here we report on the maximum likelihood estimates; the Bayesian estimates are not materially different and are reported in Appendix B.

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4.2 Results

4.2.1 Realised AC densities with many activity centers

A striking feature of realised AC density surface estimates shown in Figure 6 is that no matter where the array is placed, the region away from the array has a flat estimated density (which approaches the mean estimated density). Within the array, the realised AC surface estimate does a reasonable job of picking out the features of the Mona Lisa, but if we look at the region common to all arrays (within the dashed rectangle) we see that the realised AC surface estimate of this region is quite different for the four arrays. Estimates of the realised AC surface depend very strongly on where an array is placed. (Recall that in these

simulations the true ACs are in exactly the same place for all surveys so none
of the difference is attributable to ACs being in different places.)

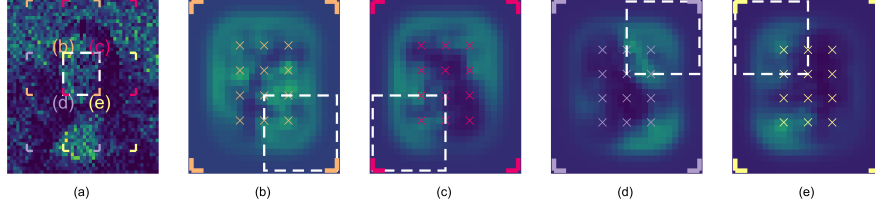


Figure 6: Plot (a) shows the true AC densities. Plots (b), (c), (d) (e) show the estimated realised AC surfaces estimated using a 4×3 array placed at four different locations. The orange, red, grey and yellow corner marks in plots (b) to (e) indicate the location of each of (b) to (e) in plot (a). The white dashed box located in the centre of the Mona Lisa's face in plot (a) is also shown in plots (b) to (d) so that one can easily compare the predictions of the centre of the face from each array.

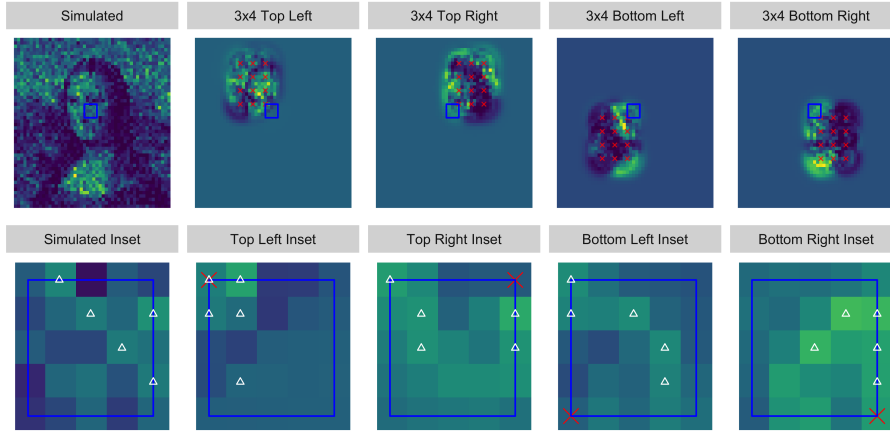


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4.2.2 Expected activity center densities with many activity centers

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 8). Recovery will seldom be this good in reality - we have covariates
that are more strongly related to true density than would usually be obtainable.
Notwithstanding this, it is true in general that because the expected AC surface

308 depends on the relationship between the covariate and density, the model uses
 309 estimates of this relationship obtained where it has lots of information (within
 310 the array) to infer density beyond the array. With our “Strong” covariate we
 311 recovered all of the broad features of the Mona Lisa, and many of the fine scale
 312 features such as eyes, shading of clouds, *etc.* With the “Moderate” covariate we
 313 recovered broad scale features but no finer details. Importantly, the estimates
 314 within the dashed rectangle are almost identical for all array placements - these
 315 estimates are not sensitive to where the array is placed.

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316 4.2.3 AC densities with fewer activity centers

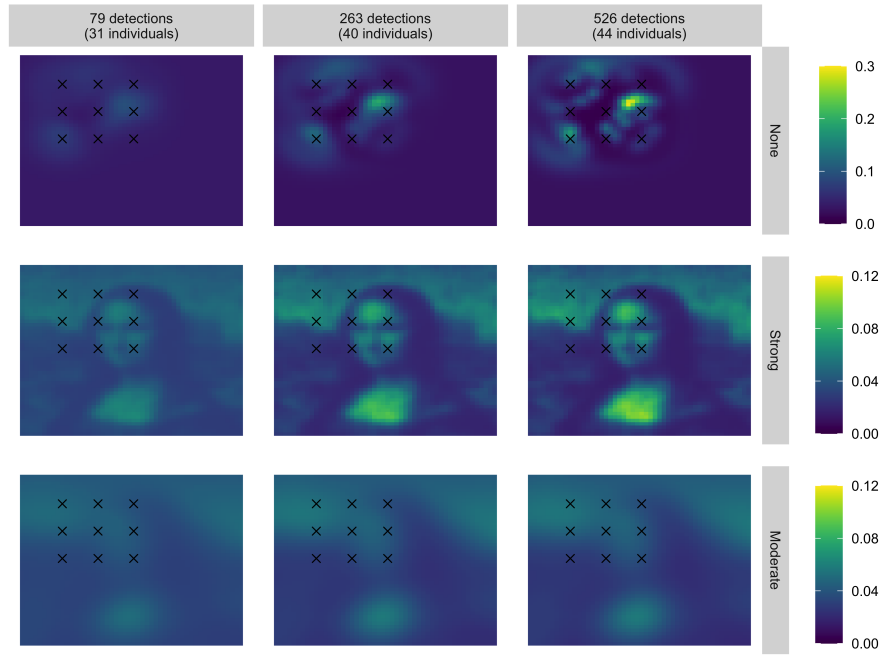


Figure 8: Estimates of realised AC density surfaces from a constant density model (first row) and expected activity center density surfaces from a model with density depending on “Strong” or “Moderate” covariates (second and third rows respectively). The 84 realised activity centers are shown in the “Realisation 2” plot of Figure 5. Detectors are shown as crosses.

317 Figure 8 shows the average realised AC density (top row) and the expected
 318 AC density (middle and bottom rows) for smaller sample sizes from 100 simu-

lations. An average of 31, 40 and 44 of the 84 ACs present in “Realisation 2” of Figure 5 was detected, giving average numbers of detections of each detected individual of 2.5, 6.6 and 12, respectively.

Notice that the estimates of the realised AC surface (top row) (a) do not really recover the Mona Lisa in any recognisable way, (b) become more “spiked” (density concentrated more closely around ACs) inside the array as sample size increases, and (c) predict flat density far from the array. We discuss each of these features below.

Regarding (a), realised AC surfaces are not designed to recover the expected density (which is what the Mona Lisa image is), they are designed to estimate the location of ACs and reflect the uncertainty in this estimation. Point (b) is a consequence of this: as sample size increases, the amount of information on where the ACs in the vicinity of the detectors are increases and hence the probability density of AC location contracts about the AC locations. Point (c) is another consequence: because 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.

We also note that because Figure 5 shows estimates averaged over 100 simulations, the realised AC densities in the plot are smoother than would be obtained from any single survey. An example from a single survey is shown in Figure 9.

Estimates of the expected AC density surface recover the Mona Lisa image well in the “Strong” covariate relationship scenarios (middle row of Figure 8), with greater focus as sample size increases and hence the amount of information about the relationship increases. The same is true in the case of the “Moderate” covariate scenarios (bottom row), but with a weaker relationship between covariate and true density, the image is more blurred, i.e. the covariate cannot pick out the high-resolution features of the density surface.

4.2.4 Realised usage densities with few activity centers

Estimates of realised usage density surface estimates are shown in Figure 9. (Note that colour key for the realised usage surfaces is on a log scale in Figure 9.) The realised usage surfaces add an encounter function that is fairly insensitive to sample size, around the realised AC surface (see Appendix A for details). This dilutes the effect of the realised AC surface concentrating around ACs as sample size increases and results in a smoother surface. Realised usage surfaces are higher than realised AC surfaces because each single AC generates multiple points of usage.

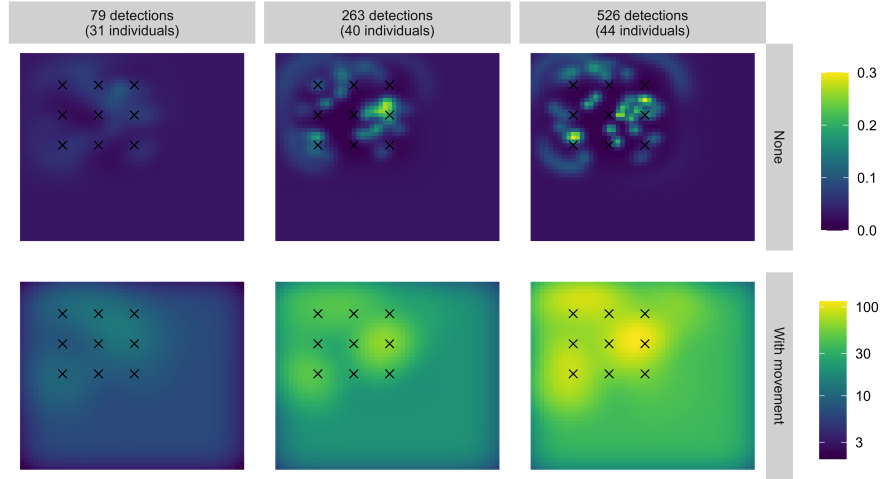


Figure 9: Estimates of realised AC density surfaces from a constant density model (first row) and the corresponding realised usage surfaces (second row), for both observed and unobserved animals. Detectors are shown as crosses.

5 Camera-trap survey of tigers in Nagarahole, India

5.1 Materials and methods

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 Dorazio & Karanth (2017). A description of the survey can be found in ?. It used an array of 162 motion-activated camera traps, these being placed at 2–3 km intervals throughout the area (Figure 10, “All traps”).

We fit a model assuming constant density, using three different trap arrays. The first array was the same one used in the original study, and from these data we estimate both the realised AC density and the realised usage density. The second array was a subset of traps that excluded about 70% of the traps, leaving a large region without traps in the interior of the study region (Figure 10, “Subset #1”). The third used subset of traps that excluded eight detectors from each of two interior areas of the survey area in which the original survey showed the realised AC density to be particularly high (Figure 10, “Subset #2”).

We also fitted a number of covariate models to the three arrays. We investigated models in which density depended on longitude and latitude, as smooths or linear effects. The model selected by AIC included a linear effect of latitude only, and we report results from this model.

5.2 Results

5.2.1 Realised activity center densities

The full array of traps used in the original Nagarahole study clearly showed three areas of high realised AC center density in the interior of the study region, along easting ≈ 625 and northing $\approx 1,324, 1,330, 1,336$, respectively (Figure 10, “All traps, no cov.”).

When we refitted using a subset of traps that excludes traps in the interior of the study region, high realised AC 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 10, “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 10, “Subset #1, no cov.”).

391 With the second subset of traps, which exclude eight detectors from each of
 392 two high density interior areas, the constant density model still recognized that
 393 activity centers are located in these areas, but the estimated locations of these
 394 activity centers showed a clear shift from what was found in the original survey
 395 (Figure 10, “Subset #2, no cov.”). The estimated location of the northernmost
 396 of the two activity centers moved to the south east, while the other activity
 397 center moved to the south.

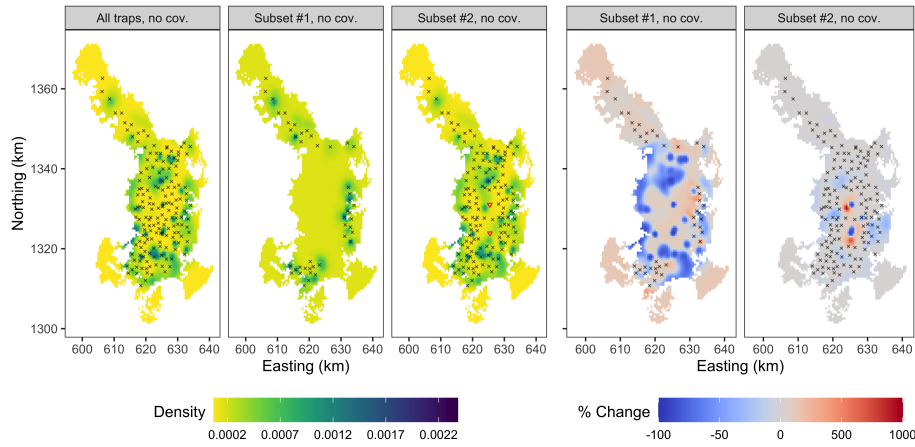


Figure 10: Estimated realised activity center densities of tigers in Nagarahole Tiger Sanctuary, India, obtained using different camera trap arrays. Plots (a), (b), and (c) show estimated densities; plots (d) and (e) show differences between the estimated densities obtained using trap subset #1 and #2 and those obtained using all traps. Detectors are shown as black crosses. Red triangles in (c) show the location of what were two high-density spots in (a).

398 5.2.2 Expected activity center densities

399 The model with the lowest AIC was one in which density depends linearly on
 400 latitude. The expected AC density surface obtained from this model showed
 401 the estimated density increasing southwards across the region, with density in
 402 the extreme south roughly four times that in the extreme north (Figure 11, “All
 403 traps, northing”). Estimates of expected AC density are much less spatially
 404 variable than estimates of realised AC density, and are much less sensitive to
 405 changes in the array of traps, providing that the array gives sufficient coverage

of the covariate space to estimate the covariate relationship (Figure 11, “Subset #1, northing” and “Subset #2, northing”).

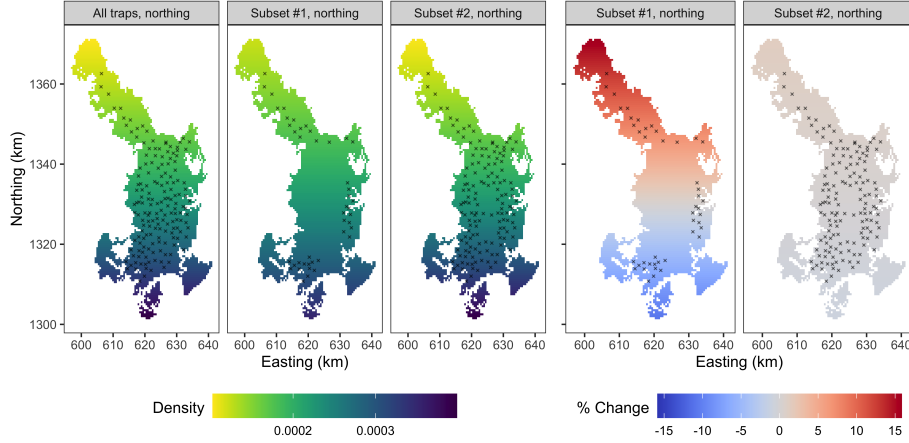


Figure 11: Estimated expected AC density of tigers in Nagarhole Tiger Sanctuary, India, obtained using different camera trap arrays. Plots (a), (b), and (c) show estimates of expected AC densities; plots (d) and (e) show differences between these when using using trap subset #1 and #2, and those obtained using all traps. Detectors are shown as black crosses. The colour scale for (d) and (e) is the same as that for plots (d) and (e) of Figure 10.

5.2.3 Realised usage densities

An estimate of the realised usage density surface is shown alongside that of the realised AC density surface in Figure 12 (note that the colour scales for the two plots are different). The realised usage density surface is smoother than the realised AC density surface, as expected - because animals “spread” themselves about their ACs by moving within their home ranges.

6 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. TA species distribution model will tend to place higher densities

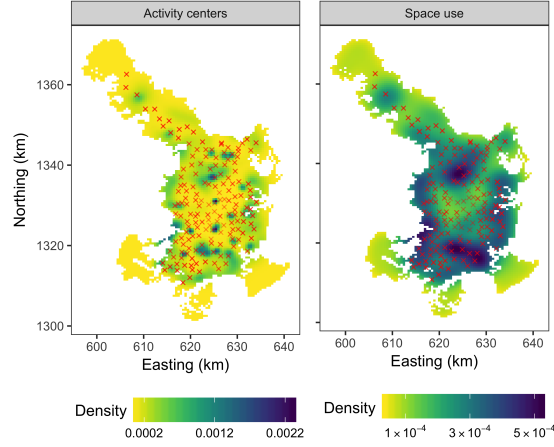


Figure 12: Estimated (a) realised activity center density surfaces from a constant density model and (b) realised animal density surfaces for tigers in Nagarhole Tiger Sanctuary, India. High density areas are indicated in blue, low density areas in yellow. Detectors are shown as red crosses.

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

436 fundamentally incorrect conclusions.

437 Realised AC surfaces tend to be flat away from where detectors are located.
 438 It is important to understand that this flatness reflects a lack of knowledge about
 439 the density surface away from detectors, and does not mean that the density
 440 surface is flat away from detectors. This point is clearly stated in Royle, Chan-
 441 dler, Sollman & Gardner (2013)² but is misinterpreted whenever researchers
 442 explicitly or implicitly treat realised activity center densities as maps of the
 443 spatial distribution of activity centers across the study area.

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

450 When considering realised ACs, SCR models answer the question “where is
 451 an animal with *this* spatial capture history likely to have its activity center?”
 452 The answer is always contingent on where detectors are located - because the
 453 capture history depends on where the detectors are located. This is the case
 454 regardless of whether one works in a Bayesian or frequentist framework. The
 455 same is true of the realised AC density surface, which simply sums estimated
 456 activity centers across animals. In this case the question being addressed is
 457 “Where are the animals with *these spatial capture histories* likely to have *their*
 458 activity centers?” The dependency on detector location applies to activity cen-
 459 ters estimated for detected animals and for those that were not detected. In
 460 the latter case we have limited information and the answer to the question for
 461 them is really just “nowhere near where detectors are located”.

462 None of this precludes realised AC density surfaces from being useful sources

²They say: “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” (p165-166 Royle *et al.*, 2013)

463 of information, but they do need to be interpreted with care. For practical
464 purposes this means always interpreting them with the caveat that they depend
465 on where detectors are located. Realised AC densities do not give proper answers
466 to questions like “where are the high- and low-density regions?” because the
467 highest and lowest points of the surface will always be at or near detectors; not
468 because these are high- or low-density regions of space, but because this is where
469 the capture histories make us most certain that animals are, or are not, present.
470 They also cannot answer questions like “are animals clustered in space?” or
471 “is animal density heterogeneous?” because the realised density surface will
472 always exhibit variability, even if animal densities are truly a realisation of a
473 homogeneous Poisson point process.

474 There is a way of using SCR so that it can be interpreted as a species
475 distribution model – by modelling the mean intensity of the underlying process
476 as a function of environmental covariates. Covariates allow one to see beyond the
477 spatial extent of the array (see Figure 8), provided that the relationship between
478 covariate and response is a good one, and that detectors cover a sufficient range
479 of covariate values to estimate that relationship well. The resulting surfaces
480 are no longer strongly tied to one particular realisation of the Poisson process.
481 Rather, they show the (estimated) intensity of the underlying process assumed
482 to generate activity centers. These expected densities will be highest where
483 environmental covariates are most favourable (such as further south in Figure
484 11). They answer the questions “Where are the high- and low-density regions?”
485 and “What spatial variables are good predictors of the high- and low-density
486 regions?” in a way that is consistent with how this question is answered by
487 species distribution models.

488 Using covariate models, and associated model-based inference, is not without
489 issues – there is a danger of extrapolating the density surface beyond the range of
490 covariates around the detectors, and the relationship with density and covariate
491 is assumed to be the same everywhere as it is around the detectors. The extent
492 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.

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,

523 with density a function of covariates, should be used.

524 7 Conclusions

525 Our main messages are:

- 526 1. Realised activity center density surfaces cannot be interpreted as SDMs.
527 This is both because these surfaces draw inferences about one realisation
528 of a spatial point process, whereas SDMs make inferences about the long
529 run average of the process; and because the surface depends systematically
530 on where detectors are located.
- 531 2. The realised activity center density surface typically shows highest peaks
532 and deepest troughs close to the center of arrays, defaulting to close to
533 the mean of the underlying process away from the array. A flat density
534 away from detectors reflects a lack of knowledge, and not constant density.
535 We should expect that in reality some areas away from detectors have
536 substantial deviations from the process mean – it is just that we do not
537 know which areas.
- 538 3. An SCR model that models mean activity center density as a function
539 of environmental covariates can be interpreted as a SDM. Here the key
540 difference is that the surface obtained from the covariate model – what we
541 call an expected activity center surface – is a statement about the mean
542 intensity of the underlying process, and is independent of array location
543 provided that the environmental covariate space has been sufficiently sam-
544 pled.
- 545 4. Realised activity center densities can be extended into realised usage den-
546 sities. This is done by using the estimated encounter or detection function
547 to “spread” animals about their estimated ACs according to the expected
548 number of encounters of the animal as distance from its AC increases.

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Appendices

A Realised AC and usage density surfaces

This appendix defines the realised activity centre (AC) surface and the realised usage surface. Let \mathbf{x} be an AC location (a point in the survey region, which has surface area A), $\boldsymbol{\omega}$ be a spatial capture history, and $f(\mathbf{x})$ be the probability density function (PDF) of \mathbf{x} ($f(\mathbf{x}) = 1/A$ when density is uniform in the survey region). The PDF of \mathbf{x} , given $\boldsymbol{\omega}$ for a single animal is then

$$f(\mathbf{x}|\boldsymbol{\omega}) = \frac{P(\boldsymbol{\omega}|\mathbf{x})f(\mathbf{x})}{\int P(\boldsymbol{\omega}|\mathbf{x})f(\mathbf{x}) d\mathbf{x}}.$$

where integration is over the whole survey region.

The realised AC density when there are N animals in the region, of which n are detected and the i th detected animal has capture history $\boldsymbol{\omega}_i$ is defined as

$$f(\mathbf{x}|\boldsymbol{\Omega}) = \sum_{i=1}^n f(\mathbf{x}|\boldsymbol{\omega}_i) + (N - n)f(\mathbf{x}|\boldsymbol{\omega}_0)$$

where $\boldsymbol{\Omega} = (\boldsymbol{\omega}_1, \dots, \boldsymbol{\omega}_n)$ and $\boldsymbol{\omega}_0$ is the zero capture history (not detected at any detector).

Now let $\mu(\mathbf{u}|\mathbf{x})$ at a point \mathbf{u} in the plane be an animal's expected usage of the point, given that an animal has its AC at the point \mathbf{x} . We define the realised usage density of the animal at \mathbf{u} , given its capture history $\boldsymbol{\omega}$ to be

$$u(\mathbf{u}|\boldsymbol{\omega}) = \int \mu(\mathbf{u}|\mathbf{x})f(\mathbf{x}|\boldsymbol{\omega}_i) d\mathbf{x},$$

where integration is over the whole survey region.

The realised usage density for the population of N animals is then defined as

$$u(\mathbf{x}|\boldsymbol{\Omega}) = \sum_{i=1}^n u(\mathbf{x}|\boldsymbol{\omega}_i) + (N - n)u(\mathbf{x}|\boldsymbol{\omega}_0).$$

586 To implement this, we discretize the survey region into a mesh of M pixels
 587 and set the expected usage function $\mu(\mathbf{u}_m|\mathbf{x})$ for pixel \mathbf{u}_m ($m = 1, \dots, M$) to
 588 be equal to the encounter function (the expected number of times an animal
 589 with AC at \mathbf{x} visits the pixel). In our application we used

$$\mu(\mathbf{u}_m|\mathbf{x}) = \lambda_0 \exp \left\{ -\frac{\|\mathbf{x} - \mathbf{u}_m\|^2}{2\sigma^2} \right\}.$$

590 B Bayesian Inference

591 *This appendix remains to be created.*