\mathbf{secr} - spatially explicit capture—recapture in R

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This document provides an overview of **secr** 2.3, an R package for spatially explicit capture–recapture analysis (SECR). It includes some background on SECR, an outline of the package, and a more detailed description of how models are implemented. See Appendix 1 for a glimpse of **secr** in action. For details of how to use **secr** see the help pages and vignettes.

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Introduction to SECR

Spatially explicit capture—recapture (SECR) is a set of methods for modelling animal capture—recapture data collected with an array of 'detectors'. Their main use is in estimating population density, but they also have advantages over non-s[atial methods when the goal is to estimate population size. SECR methods overcome edge effects that are problematic in conventional capture—recapture estimation of animal populations (Otis et al. 1978). Detectors may be live-capture traps, with animals uniquely tagged, sticky traps or snags that passively sample hair, from which individuals are distinguished by their microsatellite DNA, or cameras that take photographs from which individuals are recognized by their natural marks. The concept of a detector extends to polygons or transects that are searched for animals or their sign.

The primary data for SECR are (i) the locations of the detectors, and (ii) detections of known individuals on one or more sampling occasions (i.e. their detection histories). The generic terms 'detector' and 'detections' cover several possibilities (see 'Detector types' below); we use them interchangeably with the more specific and familiar terms 'traps' and 'captures'. Table 1 gives a concrete example of trapping data (the structure differs for detectors that are not traps).

In SECR, a spatial model of the population and a spatial model of the detection process are fitted to the spatial detection histories. The resulting estimates of population density are unbiased by edge effects and incomplete detection (other sources of bias may remain). Inverse prediction (IP SECR) and maximum likelihood (ML SECR) are alternative methods for fitting the spatial detection model (Efford 2004, Borchers and Efford 2008). Of these, ML SECR is the more flexible, with a caveat for data from single-catch traps. Data augmentation and Markov chain Monte Carlo (MCMC) methods have also been

Table 1: Example of spatially explicit detection data. Each entry (e.g. A9) records the detector at which a known animal (ID) was observed at each sample time (occasion). '.' indicates no detection. Each detector has known x-y coordinates. Formats for data input are described in 'secr-datainput.pdf'

	Occasions				
ID	1	2	3	4	5
1	A9				
2	A12	A12			
3			C6	B5	
4			G3		F3
etc.					

used for SECR (Royle and Young 2008, Royle et al. 2009, Singh et al. 2010), but this approach is orders of magnitude slower than ML SECR and easy to misuse; it is not considered here.

State and observation models

Like other statistical methods for estimating animal abundance (Borchers et al. 2002), SECR combines a state model and an observation model. The state model describes the distribution of animal home ranges in the landscape, and the observation model (a spatial detection model) relates the probability of detecting an individual at a particular detector to the distance of the detector from a central point in each animal's home range. The distances are not observed directly (usually we don't know the range centres), so conventional distance sampling methods do not apply.

Distribution of home-range centres

The distribution of range centres in the population (Borchers and Efford 2008) will usually be treated as a homogeneous Poisson point process (Fig. 1). Density is the sole parameter of a Poisson process. An inhomogeneous distribution may also be fitted; this provides a means to evaluate the effects of habitat variables on density.

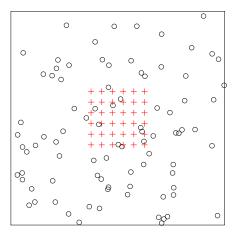


Figure 1: Hypothetical Poisson distribution of range centres near an array of detectors. We estimate the intensity (density) of this distribution.

Detection functions

A detection model uses one of several possible parametric forms for the decline in detection probability with distance (d) from the home-range centre (Table 2, Fig. 2). The probability g(d) is for the 'ideal' case of just one animal and one detector; the actual probability may differ (see discussion of 'traps' under Detector Types).

Table 2: Two functions relating the probability of detection to distance (d). See ?detectfn for more.

Halfnormal
$$g(d) = g_0 \exp\left(\frac{-d^2}{2\sigma^2}\right)$$

Exponential $g(d) = g_0 \exp\left(-\frac{d}{\sigma}\right)$

Detector types

The properties of detectors are an important part of the SECR observation model. Inside **secr**, data are tagged with a detector type to ensure they are printed, plotted and analysed appropriately.

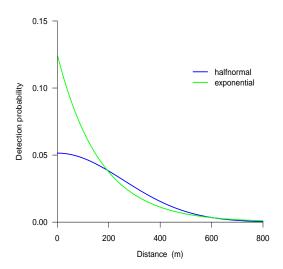


Figure 2: Alternative shapes for a function relating the probability of detection to distance from range centre.

Some common detectors (camera 'traps' and hair snags for DNA) do not capture animals, but merely record when they pass by. These 'proximity' detectors can be considered to act independently of each other. With proximity detectors, each animal × occasion 'cell' of a detection history potentially contains several positive records. In the simplest case each cell contains a binary vector coding presence or absence at each detector. A 'count' detector is a generalised proximity detector in which the data are vectors of counts, one per detector. Models for 'count' data will specify a distribution for the counts (the 'binomN' argument of secr.fit, where binomN=0 indicates Poisson, binomN=1 Bernoulli etc.).

Detectors that are true traps do not act independently because capture of an animal in one trap prevents it being caught in another trap until it is released. Traps expose animals to competing risks of capture. The per-trap probability of capture may be adjusted for the competing risk from other traps by using an additive hazard model (Borchers and Efford 2008). However, if the detectors are traps that catch only one animal at a time then there is a further level of competition – between animals for traps. Multi-catch and single-catch traps therefore represent distinct detector types. No general adjustment has been found for the per-trap probability of capture in the single-catch case (it's an open research question), and there is strictly no known maximum likelihood estimator. However, density estimates using the multi-catch likelihood for single-catch data appear only slightly biased (Efford, Borchers and Byrom 2009).

Polygon and transect detectors are for binary or count detection data (e.g.,

number of detections per animal per polygon per occasion) supplemented with the x-y coordinates of each detection (in the case of a transect it is enough to record the distance along the line). When a study uses multiple search areas or multiple transects, detections may be either independent or dependent (e.g., maximum one per animal per polygon per occasion) as with traps. The dependent or 'exclusive' type is indicated by the suffix 'X'; in this case the counts are necessarily binary. Using the 'polygonX' or 'transectX' detector type ensures that a competing-risk model is fitted.

Acoustic 'signal strength' detectors produce a binary detection vector supplemented by measurements of signal strength, as from an array of microphones.

From **secr** 2.2 there is limited support for 'unmarked' and 'presence' detector types, but these are not yet documented.

Table 3: Detector types

single	traps that catch one animal at a time
multi	traps that may catch more than one animal at a time
proximity	records presence at a point without restricting movement
count	proximity detector allowing >1 detection per animal per time
polygon	counts from searching one or more areas
transect	counts from searching one or more transects
$\operatorname{polygon} X$	binary data from mutually exclusive areas
transect X	binary data from mutually exclusive transects
signal	detections and signal strengths at multiple microphones

Origins and outline of the package 'secr'

The program DENSITY (Efford et al. 2004, Efford 2009) provides a graphical interface to SECR methods that has been accepted by many biologists. However, DENSITY has significant drawbacks: it requires the Windows operating system and is increasingly difficult to maintain, its algorithms are not always transparent or well-documented, it fits only homogeneous Poisson models, and it omits some recent advances in SECR.

The R package **secr** was written to address these weaknesses and allow for further development. It implements almost all the methods described by Borchers and Efford (2008), Efford et al. (2009), and Efford (2011). **secr** uses external C code for computationally intensive operations. Appendix 2 compares the features of DENSITY and **secr**. The important functions of **secr** are listed in Appendix 3.

How secr works

secr defines a set of R classes¹ and methods for data from detector arrays. The essential classes are:

traps locations of detectors; detector type ('proximity', 'multi', etc.)

capthist spatial detection histories, including a traps object

mask points on habitat mask secr fitted SECR model.

To perform an SECR analysis you explicitly or implicitly construct each of these objects in turn, using the functions provided (e.g., read.capthist², secr.fit). Fig. 3 summarizes the relationships among the core object classes. The classes traps (not shown), capthist and mask may optionally store covariates specific to detectors, animals and habitat points respectively. Each set of covariates is saved in a dataframe that is an attribute of the corresponding object; the covariates method is used to extract or replace covariates.

Input

Data input is covered in the separate document 'secr-datainput.pdf'. One option is to use text files in the formats used by DENSITY; these accommodate most types of data. Two files are required, one of detector (trap) locations and one of the detections (captures) themselves; the function read.capthist reads both files and constructs a capthist object. Previously (before secr 1.4) it was necessary to construct the capthist object in two stages, first making a traps object (with read.traps) and a captures dataframe, and then combining these with make.capthist. This route is still available for tricky datasets.

Output

The output from the function secr.fit is an object of class secr. This is an R list with many components. Assigning the output to a named object (such as secr0 or secrb in the example of Appendix 1) saves both the fit and the data for further manipulation. Typing the name at the R prompt invokes print.secr which formats the key results. These include the dataframe of estimates from the

¹Technically, these are S3 classes. A 'class' specifies a particular type of data object and the functions (methods) by which it is manipulated (computed, printed, plotted etc). See the R documentation for further explanation

²Text in teletype font refers to R objects that are documented in online help for the secr package, or in base R. A good place to start is the page for secr.fit

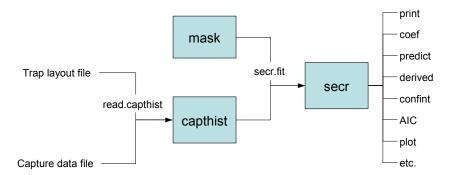


Figure 3: Essentials of the secr package. Each object class (shaded box) comes with methods to display and manipulate the data it contains (e.g. print, summary, plot, rbind, subset). The function read.capthist forms a traps object from the trap layout data and saves it as an attribute along with the capture data in a capthist object. If a habitat mask is not provided, one will be generated automatically by secr.fit. Any of the objects input to secr.fit may include a dataframe of covariates whose names may be used in a model formula. Fitted secr models may be further manipulated with the methods shown on the right. Additional functions (not shown) construct a regular detector array (e.g. make.grid, make.circle), form a mask from a traps object (make.mask), or simulate detection of a known population (sim.capthist).

predict method for secr objects. Functions are provided for further computations on secr objects (e.g., profile-likelihood confidence intervals, AIC model selection, model averaging, likelihood-ratio and score tests). Many of these are listed in Appendix 3.

One system of units is used throughout **secr**. Distances are in metres and areas are in hectares (ha). The unit of density is animals per hectare. 1 ha = $10000 \text{ m}^2 = 0.01 \text{ km}^2$. To convert density to animals / km², multiply by 100.

Documentation

The primary documentation for **secr** is in the help pages that accompany the package. Help for a function is obtained in the usual way by typing a question mark at the R prompt, followed by the function name. Note the 'Index' link at the bottom of each help page – you will probably need to scroll down to find it.

The consolidated help pages are also distributed as the file secr-manual.pdf. Searching this text is a powerful way to locate a function for a particular task.

It may be accessed from within R using

```
> RShowDoc("secr-manual", package = "secr")
```

Other documentation in the form of pdf files based on Sweave vignettes will be added from time to time. The 'directory' link in the package help index lists available files. Each pdf file may be accessed by clicking on the link or with RShowDoc() as above. These vignettes are included in secr 2.3³:

```
secr-overview.pdf this document
secr-datainput.pdf data formats and input functions
secr-densitysurfaces.pdf modelling density surfaces
secr-finitemixtures.pdf mixture models for individual heterogeneity
secr-sound.pdf analysing data from microphone arrays
secr-polygondetectors.pdf using polygon and transect detector types
```

The web page http://www.otago.ac.nz/density/ should be checked for news of bug fixes and new releases. New versions will be posted on CRAN http://cran.r-project.org/, but there may be a delay of a few days. Help may be sought at http://www.phidot.org/forum; see also the FAQ there for DENSITY and secr. For information on changes in each version type

```
> news(package = "secr")
```

Models in secr

The next three sections are fairly heavy going: on your first time through you may want to skip to 'Specifying effects on detection parameters'.

A family of capture—recapture models, such as the Cormack-Jolly-Seber models for survival, may include submodels⁴ that allow for variation in core ('real') parameters, including the effects of covariates. Annual survival, for example, may vary with the severity of winter weather, so it often makes sense to include a measure of winter severity as a covariate. Gary White's MARK software has been particularly successful in packaging open-population models for biologists, and **secr** aims for similar flexibility.

The language of generalised linear models is convenient for describing submodels (e.g. Huggins 1989, Lebreton et al. 1992). Each parameter is treated as a linear combination of predictor variables on its transformed ('link') scale.

³The Sweave Rnw files are available on request

⁴This use of 'submodel' is non-standard – maybe we'll find a better term

This is useful for combining effects because, given a suitable link function, any combination maps to a feasible value of the parameter. The logit scale has this property for probabilities in (0, 1), and the natural log scale works for positive parameters i.e. $(0, +\infty)$. These are the link functions used most often in **secr**, but there are others, including the identity (null) link.⁵

Submodels are defined symbolically in **secr** using R formula notation. A separate linear predictor is used for each core parameter. Core parameters are 'real' parameters in the terminology of MARK, and **secr** uses that term because it will be familiar to biologists. Four real parameters are commonly modelled in **secr** 2.3; these are denoted D (for density), g0, sigma and z. Only the last three real parameters, which jointly define the model for detection probability as a function of location, can be estimated directly when the model is fitted by maximizing the conditional likelihood (CL = TRUE in **secr.fit**). D is then a derived parameter that is computed from an **secr** object with the function derived or one of its siblings (derived.cluster etc.). 'z' is a shape parameter that is used only when the detection function has three parameters (annular halfnormal, cumulative gamma, hazard-rate etc. – see ?detectfn).

For each real parameter there is a linear predictor of the form $\mathbf{y} = \mathbf{X}\beta$, where \mathbf{y} is a vector of parameter values on the link scale, \mathbf{X} is a design matrix of predictor values, and β is a vector of coefficients. Each element of \mathbf{y} and corresponding row of \mathbf{X} relates to the value of the real parameter in a particular circumstance (e.g. density at a particular point in space, or detection probability of an animal on a particular occasion). The elements of β are coefficients estimated when we fit the model. In MARK these are called 'beta parameters' to distinguish them from the transformed 'real' parameter values in \mathbf{y} . secr acknowledges this usage, but also refers to beta parameters as 'coefficients' and real parameters as 'fitted values', a usage more in line with other statistical modelling in \mathbf{R} . \mathbf{X} has one column for each element of β . Design matrices are described in more detail in the next section.

Design matrices

A design matrix is specific to a 'real' parameter. Each design matrix \mathbf{X} contains a column of '1's (for the constant or intercept term) and additional columns as needed to describe the effects in the submodel for the parameter. Depending on the model, these may be continuous predictors (e.g. air temperature to predict occasion-to-occasion variation in g0), indicator variables (e.g. 1 if animal i was caught before occasion s, 0 otherwise), or coded factor levels. Within secr.fit, each design matrix is constructed automatically from the input data and the model formula in a 2-stage process.

⁵Set link functions with the link argument of secr.fit.

First, a data frame is built containing 'design data' with one column for each variable in the formula. Second, the R function model.matrix is used to construct the design matrix. This process is hidden from the user. The design matrix will have at least one more column than the design data; there may be more if the formula includes interactions or factors with more than two levels. For a good description of this general approach see the documentation for RMark (Laake and Rexstad 2008). The necessary design data are either extracted from the inputs or generated automatically, as explained in later sections. 'Real' parameters fall into two groups: density (D) and detection (g0, sigma and z). Density and detection parameters are subject to different effects, so they use different design matrices as described in the next three sections.

Detection submodels

For SECR, we want to model the detection of each individual i on occasion s at detector k. Given n observed individuals on S occasions at K detectors, there are therefore nSK detection probabilities of interest. We treat these as elements in a 3-dimensional array. Strictly, we are also interested in the detection probabilities of unobserved individuals, but these are estimated only by extrapolation from those observed so we do not include them in the array.

In a null model, all nSK detection probabilities are assumed to be the same. The conventional sources of variation in capture probability (Otis et al. 1978) appear as variation either in the n dimension ('individual heterogeneity' h), or in the S dimension ('time variation' t), or as a particular interaction in these two dimensions ('behavioural response to capture' b). Combined effects are possible. SECR introduces additional complexity.

Detection probability in SECR is no longer a scalar (even for a particular animal-occasion-detector combination); it is described by a 'detection function'. The detection function may have two parameters (e.g. g0, sigma for a half-normal function), or three parameters (e.g. g0, sigma, z). Any of the parameters of the detection function may vary with respect to individual (subscript i), occasion (subscript s) or detector (subscript k).

The full design matrix for each detection submodel has one row for each combination of i, s and k. Allowing a distinct probability for each animal (the n dimension) may seem excessive, and truly individual-specific covariates are feasible only when a model is fitted by maximizing the conditional likelihood (cf Huggins 1989). However, the full nSK array is convenient for coding both group membership (Lebreton et al. 1992, Cooch and White 2008) and experience of capture, even when individual-specific covariates cannot be modelled.

The programming gets even more complex. Analyses may combine data from

several independent samples, dubbed 'sessions'. This adds a fourth dimension of length equal to the number of sessions. When finite mixture models are used for detection parameters there is even a fifth dimension, with the preceding structure being replicated for each mixture class. Fortunately, **secr** handles all this out of view: as a user you only need to know how to specify the detection model, which we describe next.

Specifying effects on detection parameters

Effects on parameters of detection probability are specified with R formulae. The variable names used in formulae are either names for standard effects (Table 4) or the names of user-supplied covariates. Effects 'b', 'B', 'bk', and 'Bk' refer to individuals whereas 'k' and 'K' refer only to sites. Groups ('g') are used only in models fitted by maximizing the full likelihood; for conditional likelihood models use a factor covariate to achieve the same effect.

Table 4: Automatically generated predictor variables used in detection models

Variable	Description	Notes
g	group	interaction of the capthist individual covari-
		ates listed in argument groups of secr.fit
\mathbf{t}	time factor	one level for each occasion
${ m T}$	time trend	linear trend over occasions on link scale
b	learned response	step change after first detection
В	transient response	depends on detection at preceding occasion
		(Markovian response)
bk	animal x site response	site-specific step change
Bk	animal x site response	site-specific transient response
k	site learned response	site effectiveness changes once any animal
		caught
K	site transient response	site effectiveness depends on preceding occa-
		sion
session	session factor	one level for each session
Session	session trend	linear trend on link scale
h2	2-class mixture	finite mixture model with 2 latent classes

Any name in a formula that is not a variable in Table 4 is assumed to refer to a user-supplied covariate. secr.fit looks for user-supplied covariates in data frames embedded in the capthist argument or supplied in the timecov and sessioncov arguments, using the first match (Table 5).

The formula for any detection parameter (g0, sigma, z) may be constant

Table 5: User-provided covariates used in detection models. The names of columns in the respective dataframes may be used in model formulae

Covariate type	Data source	Notes
Individual	covariates(capthist)	conditional likelihood
Time	timecov argument	
Detector	<pre>covariates(traps(capthist))</pre>	
Session	sessioncov argument	

Table 6: Some examples of the model argument in secr.fit

Model	Description		
g0 \sim 1	g0 is constant across animals, occasions and detec-		
	tors		
g0 \sim b	learned response affects $g0$		
list(g0 \sim b, sigma \sim b)	learned response affects both g0 and sigma		
g0 \sim h2	2-class finite mixture for heterogeneity in g0		
g0 \sim b + T	learned response in g0 combined with trend over oc-		
	casions		
$\texttt{sigma} \sim \texttt{g}$	detection scale sigma differs between groups		
$\texttt{sigma} \sim \texttt{g*T}$	group-specific trend in sigma		
D \sim cover	density varies with 'cover' given in covari-		
	ates(mask)		
list(D \sim g, g0 \sim g)	both density and g0 differ between groups		
D \sim session	session-specific density		

(\sim 1, the default) or some combination of terms in standard R formula notation (see ?formula). For example, g0 \sim b + T specifies a model with a learned response and a linear time trend in g0; the effects are additive on the link scale. See Table 6 for other examples.

For other effects, the design matrix for detection parameters may also be provided manually in the argument dframe of secr.fit. This feature is untested.

Density submodels

The SECR log likelihood is evaluated by summing values at points on a 'habitat mask' (the mask argument of secr.fit). Each point in a habitat mask represents a grid cell of potentially occupied habitat (their combined area may be almost any shape). The full design matrix for density (D) has one row for each point in the mask. As for the detection submodels, the design matrix has one

column for the intercept (constant) term and one for each predictor.

Predictors may be based on Cartesian coordinates (e.g. 'x' for an east-west trend), a continuous habitat variable (e.g. vegetation cover) or a categorical (factor) habitat variable. Predictors must be known for all points in the mask (non-habitat excluded). The variables 'x' and 'y' are the coordinates of the habitat mask and are automatic, as are 'x2', 'y2', and 'xy'. Other spatial covariates should be named columns in the covariates attribute of the habitat mask.

See the vignette secr-densitysurfaces.pdf for more on fitting and displaying density surfaces.

Model fitting and estimation

Models are fitted in secr.fit by numerically maximizing the likelihood. The likelihood involves integration over the unknown locations of the animals' range centres. This is achieved in practice by summation over points in the habitat mask, which has some implications for the user. Computation may be slow, especially if there are many points in the mask, and estimates may be sensitive to the particular choice of mask (either explicitly in make.mask or implicitly via the buffer argument).

The default maximization algorithm is Newton-Raphson in the function stats::nlm. By default, all reported variances, covariances, standard errors and confidence limits are asymptotic and based on a numerical estimate of the information matrix. The Newton-Raphson algorithm is fast, but it sometimes fails to compute the information matrix correctly, causing some standard errors to be set to 'NA'; see the 'method' argument of secr.fit for alternatives. Use confint.secr for profile likelihood intervals and simulate.secr for parametric bootstrap intervals (both are slow).

Habitat masks

We have already introduced the idea of a habitat mask. The SECR likelihood is evaluated by summing values at points on a mask⁶; each point represents a grid cell of potentially occupied habitat. Masks may be constructed by placing a buffer of arbitrary width around the detectors, possibly excluding known non-habitat. How wide should the buffer be? The general answer is 'Wide enough not to cause bias in estimated densities'. This depends on the scale of movement of your animal, and on the chosen detection function. For specifics, see the help for mask and the various mask-related functions (make.mask, mask.check,

⁶A 'mask' in **secr** is equivalent to a 'mesh' in DENSITY

suggest.buffer, and esa.plot). Heavy-tailed detection functions such as the hazard-rate and lognormal can be problematic because they require an unreasonably large buffer for stable density estimates.

Detector clusters

For surveying large areas it is efficient to use groups of detectors: within a group the detectors are close enough that animals may be re-detected at multiple points, while groups of detectors may be distributed across a region according to a probability design. From version 2.1 secr allows for detector groups with the 'cluster' data structure. This is an attribute of a traps object that records which detectors belong to which cluster⁷.

Functions are provided to generate detector arrays with a clustered structure (trap.builder, make.systematic), to extract or replace the cluster attribute (clusterID), to compute the geometric centres and numbers of detections per cluster (cluster.centres, cluster.counts), etc.

Data from a large, clustered design may often be analysed more quickly if the capthist object is first collapsed into one using the geometry of a single cluster (the object retains a memory of the number of individuals from each original cluster in the attribute n.mash). Use the function mash for this. Functions derived, derived.mash and the method predict.secr use n.mash to adjust their output density, SE, and confidence limits.

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⁷At present, clusters are assumed to share the same geometry (number of detectors, withincluster spacing etc.)

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Appendix 1. A simple secr analysis

A simple analysis might look like this. We start by loading the package, setting the working folder, and constructing an object myCH that contains both the captures and the trap locations.

```
> library(secr)
> olddir <- setwd(system.file("extdata", package = "secr"))
> myCH <- read.capthist("capt.txt", "trap.txt", fmt = "XY")
No errors found :-)
> setwd(olddir)
```

Next we fit two simple models and compare them with AIC. We set trace = FALSE to reduce the volume of output, but the default trace = TRUE is usually better.

A model with learned trap response $(g0\sim b)$ showed no improvement in fit over a null model $(g0\sim 1)$. In this instance the estimates of density from the two models were also very close (not shown) and we rely on the null model for estimation. Before displaying the estimates we check that the likelihood is stable as we vary the mask buffer width (rows) and spacing (columns)

```
> mask.check(secr0)

Computing log likelihoods...
          7.34375 5.5078125 3.671875
100 -759.0258 -759.0248 -759.0256
150 -759.0165 -759.0165 -759.0165
200 -759.0165 -759.0165 -759.0165
```

It seems we would have been better to use a buffer slightly wider than the default (100 m), so we repeat the fit and display the results:

```
> secr.fit(myCH, model = g0 ~ 1, buffer = 150, trace = FALSE)

secr.fit( capthist = myCH, model = g0 ~ 1, buffer = 150, trace = FALSE )

secr 2.3.2, 06:16:44 15 May 2012
```

Detector type multi
Detector number 100
Average spacing 30 m

x-range 365 635 m y-range 365 635 m

N animals : 76 N detections : 235 N occasions : 5

Mask area : 32.49 ha

Model : D~1 g0~1 sigma~1

Fixed (real) : none

Detection fn : halfnormal Distribution : poisson

N parameters : 3

Log likelihood : -759.0165 AIC : 1524.033 AICc : 1524.366

Beta parameters (coefficients)

beta SE.beta lcl ucl
D 1.7001483 0.11771582 1.469429 1.9308670
g0 -0.9785242 0.13620932 -1.245490 -0.7115588
sigma 3.3800087 0.04445189 3.292885 3.4671328

Variance-covariance matrix of beta parameters

D g0 sigma
D 0.0138570141 0.0001842958 -0.001013496
g0 0.0001842958 0.0185529785 -0.003342490
sigma -0.0010134963 -0.0033424903 0.001975970

Fitted (real) parameters evaluated at base levels of covariates link estimate SE.estimate lcl ucl

```
D log 5.4747590 0.64670479 4.3467545 6.8954862 g0 logit 0.2731847 0.02704502 0.2234819 0.3292545 sigma log 29.3710266 1.30624277 26.9204064 32.0447318
```

The density estimate is $5.475~\mathrm{ha^{-1}}$ (95% confidence interval 4.35– $6.90~\mathrm{ha^{-1}}$). We can compare these estimates to those from the initial fit with a narrower buffer; estimated density differs only in the third decimal place:

> predict(secr0)

```
link estimate SE.estimate lcl ucl
D log 5.4788218 0.64671163 4.3507089 6.8994476
g0 logit 0.2731605 0.02705173 0.2234467 0.3292455
sigma log 29.3695698 1.30602242 26.9193502 32.0428102
```

Appendix 2. Software feature comparisons

 $\bullet \;$ full implementation; $\circ \;$ incomplete or inferior implementation.

Feature	DENSITY 4.4	secr 2.0	secr 2.3
General			
Graphical interface	•	0	0
Inverse prediction (IP SECR)	•	•	•
Maximum likelihood estimation (ML SECR)	•	•	•
Non-spatial closed-population estimators		•	•
Simulation of spatial sampling	•	0	0
Build detector arrays	•	0	•
Control of random number generator	0	•	•
Closure tests	0	•	•
Import or export DENSITY text files	•	•	•
Import or export SPACECAP text files		•	•
Convert BUGS data		0	0
GIS polygons as habitat mask	•	•	•
Clustered detector layouts			•
Mash data from clustered layouts			•
Upload coordinates to GPS (uses GPSBabel)			•
ML SECR			
Profile likelihood confidence intervals	•	•	•
Detectors used may vary with occasion	•	•	•
Fixed parameters	0	•	•
Parametric bootstrap	0	•	•
Between-session models	•	•	•
Mixture models for individual heterogeneity	•	•	•
Confidence ellipses	•	•	•
Formula-based model notation		•	•
Density models (inhomogeneous 2-D Poisson)		•	•
User-defined density models			•
Plot density models			•
Groups (e.g. males & females)		•	•
Score tests for model selection		•	•
Model averaging		•	•
Structural relationships between parameters		•	•
Plot likelihood surface		•	•

Empirical variance from replicate units		•	•
Mask diagnostics	0	•	•
Suggested buffer width		•	•
Contours of detection probability	•	•	•
Compute pdf for individual's range centre	•	•	•
Regional population size (region.N)			•
Detector types			
Single-catch trap ¹	0	0	0
Multi-catch trap	•	•	•
Proximity	•	•	•
Signal strength (acoustic)		•	•
Count		•	•
Polygon		•	•
Transect		•	•
Polygon (exclusive)		•	•
Transect (exclusive)		•	•
Unmarked			0
Presence/absence			0
Detection functions			
Halfnormal	•	•	•
Hazard rate ²	•	•	•
Exponential	•	•	•
Compound halfnormal		•	•
$\mathrm{Uniform^1}$	0	0	0
w-exponential		•	•
Annular halfnormal		•	•
Binary signal strength		•	•
Signal strength		•	•
Signal strength spherical		•	•
Cumulative $lognormal^2$		•	•
Cumulative gamma		•	•

 $^{^1\}mathrm{Not}$ fitted by ML SECR $^2\mathrm{Not}$ recommended because of heavy tail

Appendix 3. Functions in secr arranged according to use

This list groups the main functions of **secr** 2.3. Many functions for data manipulation and plotting are omitted. S3 methods are marked with an asterisk

Manipulate core objects

addCovariates add spatial covariates to traps or mask head* first rows of capthist, traps or mask

join combine sessions of multi-session capthist object

make.grid construct detector array

make.capthist form capthist from traps and detection data

make.mask construct habitat mask (mesh)
make.systematic construct random systematic design

MS.capthist combine capthist objects into one multisession capthist

plot* plot capthist, traps or mask
rbind.capthist append capthist objects

read.capthist input captures and trap layout from Density format, one

call

read.traps input detector locations from text file

sim.capthist simulate capture histories
subset* filter capthist, traps or mask
summary* summarise capthist, traps or mask
tail* last rows of capthist, traps or mask
trap.builder construct various complex designs

verify* check capthist, traps or mask for internal consistency

randomHabitat generates habitat mask with random landscape

Extract or replace attributes of traps object

clustertrap detector number within cluster

covariates* detector-level covariates

detector* detector type ('multi', 'proximity' etc.)

polyID* polygon or transect identifier

usage* disable detectors (occasion- and detector-specific)

Extract or replace attributes of capthist object

covariates* individual-level covariates, including grouping factors

session* session identifier(s)

traps* embedded traps object(s)

Extract detection-specific data from capthist object

alive TRUE/FALSE
animalID individual ID
clusterID cluster identifier

clustertrap detector number within cluster

occasion occasion

signal strength (signal detectors)

trap detector

xy detection coordinates (polygon and transect detectors)

Fit SECR model

ip.secr fit simple SECR model by simulation & inverse prediction secr.fit maximum likelihood fit; result is a fitted secr object

Operate on fitted secr object(s)

AIC* model selection, model weights

coef* 'beta' parameters

deviance* model deviance

df.residual* degrees of freedom for deviance

derived.nj variance from replicated sampling units
derived.cluster variance from replicated sampling units
derived.external variance from replicated sampling units
fxi.secr probability density of home-range centre

logLik*log-likelihood of fitted modelLR.testlikelihood-ratio test of two modelsmodel.averagecombine estimates using AICc weights

plot* plot detection functions with confidence bands

predict* 'real' parameters for arbitrary levels of predictor variables

predictDsurface* evaluate density surface at each point of a mask

score.test model selection with score statistic using observed informa-

tion

simulate* generate realisations of fitted model

sim.secr parametric bootstrap

vcov* variance-covariance matrix of 'beta' or 'real' parameters

Mask diagnostics

suggest.buffer find buffer width to keep bias within bounds

esa.plot cumulative plot esa vs buffer width

mask.check likelihood or estimates vs. buffer width and spacing

Specialised graphics

fxi.contour contour plot of home-range centre pdf(s)

pdot.contour contour plot of detection probability

buffer.contour concave and convex boundary strips

Convert or export data

RMarkInput convert capthist to dataframe for RMark
write.capthist export capthist as text files for DENSITY
write.DA convert capthist for analysis in WinBUGS
write.SPACECAP export capthist as text files for SPACECAP
writeGPS upload coordinates to GPS using GPSBabel

Miscellaneous

ARL asymptotic range length

autoini generate starting values of D, g0 and sigma for secr.fit closure.test closure tests of Otis et al. (1978) and Stanley & Burnham

(1999)

closedN closed population size by various conventional estimators

counts summary data from capthist object dbar mean distance between capture locations

distancetotrapfrom an arbitrary set of pointsMMDMmean maximum distance movedmovesdistances between capture locationsnearesttrapfrom an arbitrary set of points

pdot location-specific net probability of detection

RPSV 'root pooled spatial variance', a simple measure of home-

range size

Datasets - see ?datasetname for details

deermouse Peromyscus maniculatus live-trapping data of V. H. Reid

published as a CAPTURE example by Otis et al. (1978)

Wildlife Monographs 62

hornedlizard repeated searches of a quadrat in Arizona for flat-tailed

horned lizards $Phrynosoma\ mcallii$ (Royle & Young Ecology

89, 2281–2289)

housemouse Mus musculus live-trapping data of H. N. Coulombe pub-

lished as a CAPTURE example by Otis et al. (1978)

Wildlife Monographs 62

ovenbird multi-year mist-netting study of ovenbirds Seiurus auro-

capilla at a site in Maryland, USA.

ovensong acoustic detections of ovenbirds (Dawson & Efford Journal

of Applied Ecology 46, 1201–1209)

possum brushtail possum Trichosurus vulpecula live trapping at

Waitarere, North Island, New Zealand April 2002 (Efford

et al. 2005 Wildlife Society Bulletin 33, 731–738)

secrdemo simulated data captdata and some fitted models

skink multi-session lizard (Oligosoma infrapunctatum and O. li-

neoocellatum) pitfall trapping data from Lake Station, Upper Buller Valley, South Island, New Zealand (M. G. Efford,

B. W. Thomas and N. J. Spencer unpublished).

stoatDNA stoat Mustela erminea hair tube DNA data from Matak-

itaki Valley, South Island, New Zealand (Efford, Borchers

and Byrom 2009).