

secr 5.0 - spatially explicit capture–recapture in R

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This document provides an overview of **secr** 5.0, 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 `secr-tutorial.pdf` for an introductory tutorial. For details of how to use `secr` see the help pages and vignettes.

NOTE: `secr` was extensively re-written between versions 3.2 and 4.0, but the interface remained unchanged. For many datasets version 4 is significantly faster. Other changes are described in `secr-version4.pdf`.

Add-on packages extend the capability of `secr` and are documented separately. `secrlinear` enables the estimation of linear density (e.g., animals per km) for populations in linear habitats such as stream networks (`secrlinear-vignette.pdf`). `ipsecr` fits models by simulation and inverse prediction, rather than maximum likelihood; this is a rigorous way to analyse data from single-catch traps (`ipsecr-vignette.pdf`). `secrdesign` enables the assessment of alternative study designs by Monte Carlo simulation; scenarios may differ in detector (trap) layout, sampling intensity, and other characteristics (`secrdesign-vignette.pdf`).

Spatial open-population capture–recapture models are implemented in the R package `openCR` (Efford and Schofield 2020). Other open-population packages due to Ben Augustine and Richard Glennie are available on GitHub (<https://github.com/benaug/OpenPopSCR>; <https://github.com/r-glennie/openpopscr>).

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’. The methods are used primarily to estimate population density, but they also have advantages over non-spatial methods when the goal is to estimate population size (Efford and Fewster 2013). 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 areas (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).

Table 1. Some 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`.

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

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 used for SECR (Royle and Young 2008, Royle et al. 2009, Singh et al. 2010, Royle and Gardner 2011, Royle et al. 2014), but this approach is much slower than ML SECR; 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. 1a). Density (= intensity) is the sole parameter of a homogeneous Poisson process. An inhomogeneous Poisson distribution may also be fitted; this provides a means to evaluate the effects of habitat variables on density.

Detection functions

A detection model describes the decline in detection probability with distance (d) from the home-range centre (Fig. 1b). 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).

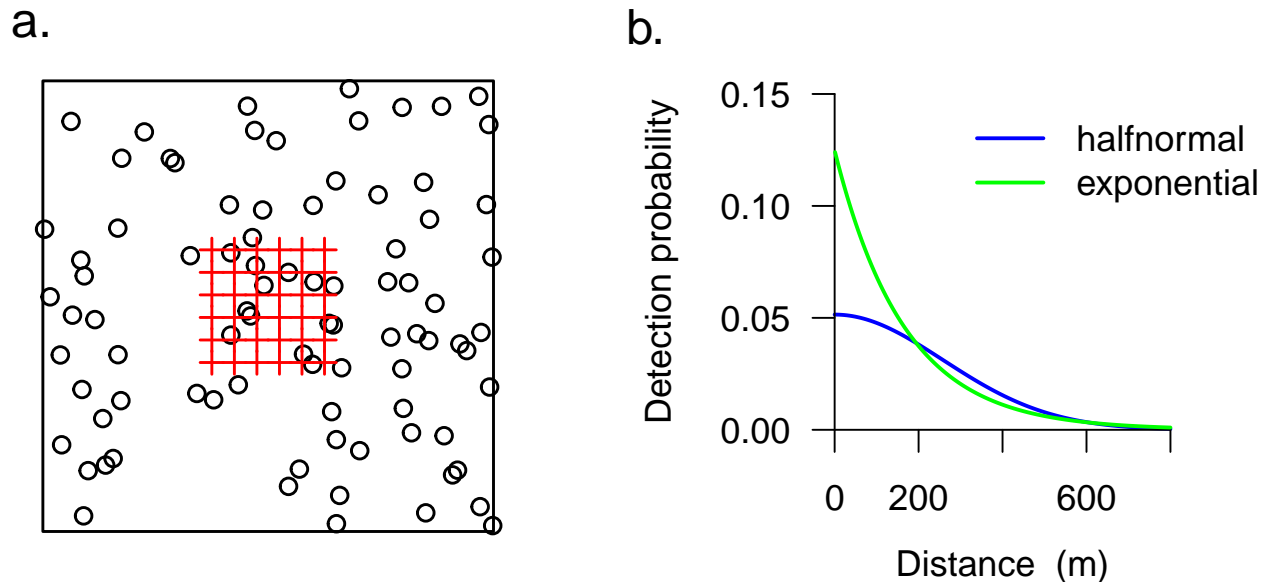


Fig. 1. (a) Hypothetical Poisson distribution of range centres near an array of detectors. Each dot represents one individual. SECR estimates the density of this distribution. (b) Alternative detection functions. The halfnormal is defined by $g(d) = g_0 \exp\left(\frac{-d^2}{2\sigma^2}\right)$ and the exponential by $g(d) = g_0 \exp\left(-\frac{d}{\sigma}\right)$. See ?detectfn for more.

Detector types

The properties of detectors are an important part of the SECR observation model (Table 2). Inside `secr`, data are tagged with a detector type to ensure they are printed, plotted and analysed appropriately.

Some common detectors (camera 'traps' and hair snags for DNA) do not capture animals, but merely record that an animal has visited a site. These 'proximity' detectors can be considered to act independently of each other. With proximity detectors, each animal \times 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 (for such binary proximity detectors each observation has a Bernoulli distribution). 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 via the ‘binomN’ argument of `secr.fit` (binomN = 0 indicates Poisson; binomN > 1 indicates binomial with size = binomN; binomN = 1 indicates binomial with size given by the ‘usage’ attribute for the detector and occasion).

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. Estimates of average density using the multi-catch likelihood for single-catch data appear only slightly biased (Efford, Borchers and Byrom 2009), and this substitution is made automatically in `secr`, with a warning. However, the substitution is imperfect when density varies (Distiller and Borchers 2015). Simulation and inverse prediction in `ipsecr` is an alternative and more robust method for single-catch data.

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. 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.

There is limited support in `secr` for the analysis of locational data from telemetry (‘telemetry’ detector type). Telemetry data are used to augment capture–recapture data (see `addTelemetry` and `secr-telemetry.pdf`).

Table 2. Detector types in `secr`

Detector	Description
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
capped	proximity detector with maximum one animal at a time
polygon	counts from searching one or more areas
transect	counts from searching one or more transects
polygonX	binary data from mutually exclusive areas
transectX	binary data from mutually exclusive transects
signal	detections and signal strengths at multiple microphones
telemetry	locations from radiotelemetry

Origins and outline of the package `secr`

The program DENSITY (Efford et al. 2004, Efford 2012) provides a graphical interface to SECR methods that was used by many biologists. However, DENSITY has significant drawbacks: it requires the Windows operating system, its algorithms are not always transparent or well-documented, it fits only homogeneous Poisson models, and it omits 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), Efford (2011), Efford and Fewster (2013), Efford et al. (2013) and Efford and Mowat (2014). **secr** 5.0 uses external C++ code via package **Rcpp** for computationally intensive operations (Eddelbuettel and Francois 2011); Multi-threading on multiple CPUs with **RcppParallel** (Allaire et al. 2021) gives major speed gains. The most important functions of **secr** are listed in Appendix 1.

How **secr** works

secr defines a set of R classes¹ and methods for data from detector arrays and models fitted to those data.

Table 3. Essential classes in **secr**.

Class	Data
traps	locations of detectors; detector type ('proximity', 'multi', etc.)
capthist	spatial detection histories, including a 'traps' object
mask	raster map of habitat near the detectors
secr	fitted SECR model

To perform an SECR analysis you explicitly or implicitly construct each of these objects in turn. Fig. 2 indicates the relationships among the classes.

¹Technically, these are S3 classes. A 'class' in R 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.

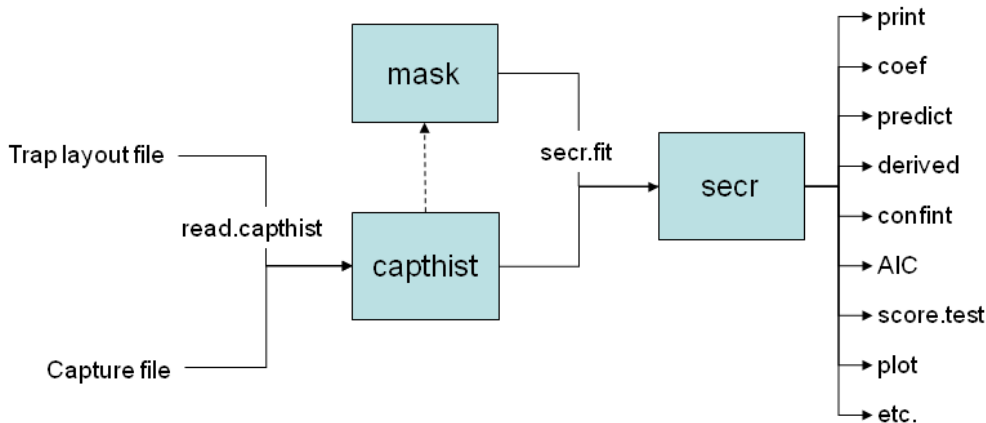


Fig. 2. Essentials of the `secr` package.

- Each object class (shaded box) comes with methods to display and manipulate the data it contains (e.g. `print`, `summary`, `plot`, `rbind`, `subset`)².
- The function `read.caphist` forms a ‘traps’ object from the detector layout data and saves it as an attribute, along with capture data read from another file, in a ‘caphist’ object.
- By default, a habitat mask is generated automatically by `secr.fit` using a specified buffer around the detectors (traps). The function `make.mask` gives greater control over this step.
- Any of the objects input to `secr.fit` (traps, caphist, mask) may include a dataframe of covariates saved as an attribute. Covariate names may be used in model formulae; the `covariates` method is used to extract or replace covariates. Use `addCovariates` for covariates from spatial data sources (e.g., shapefile or ‘sf’ object)
- Fitted `secr` models may be manipulated with the methods shown on the right and others listed in Appendix 2.

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.caphist` reads both files and constructs a caphist object. It is also possible to construct the caphist object in two stages, first making a traps object (with `read.traps`) and a captures dataframe, and then combining these with `make.caphist`. This more general route may be needed for unusual 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 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 `predict` method for `secr` objects. Functions are provided for further computations on `secr` objects (e.g., AIC model selection, model averaging, profile-likelihood confidence intervals, and likelihood-ratio tests). Many of these are listed in Appendix 2.

One system of units is used throughout `secr`. Distances are in metres and areas are in hectares (ha). The unit of density for 2-dimensional habitat is animals per hectare. $1 \text{ ha} = 10000 \text{ m}^2 = 0.01 \text{ km}^2$. To convert density to animals per km^2 , multiply by 100. Density in linear habitats (see package `secrlinear`) is expressed in animals per km.

²Text in this font refers to R objects that are documented in online help for the `secr` package, or in base R.

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 index may also be accessed with `help(package = secr)`.

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

Other documentation, in the form of pdf vignettes built with **knitr**, will be added from time to time. The ‘User guides...’ link in the package help index lists available files. The vignettes in Table 4 may be found on the Density website.

Table 4. Vignettes for **secr** 5.0.

Vignette	Topic
<code>secr-overview.pdf</code>	introduction (this document)
<code>secr-datainput.pdf</code>	data formats and input functions
<code>secr-version4.pdf</code>	what’s new in <code>secr</code> 4.x
<code>secr-tutorial.pdf</code>	tutorial using Burnham and Cushwa snowshoe hare data
<code>secr-habitatmasks.pdf</code>	habitat masks, buffer width and related topics
<code>secr-models.pdf</code>	general description of models in secr
<code>secr-troubleshooting.pdf</code>	problems with <code>secr.fit</code> , including speed issues
<code>secr-densitiesurfaces.pdf</code>	modelling density surfaces
<code>secr-finitemixtures.pdf</code>	mixture models for individual heterogeneity
<code>secr-markresight.pdf</code>	mark–resight models
<code>secr-multisession.pdf</code>	data from multiple independent sessions
<code>secr-noneuclidean.pdf</code>	non-Euclidean distance models
<code>secr-parameterisations.pdf</code>	alternative parameterisations of detection
<code>secr-polygondetectors.pdf</code>	using polygon and transect detector types
<code>secr-sound.pdf</code>	analysing data from microphone arrays
<code>secr-spatialdata.pdf</code>	tips on external spatial data and functions
<code>secr-telemetry.pdf</code>	analysing combined telemetry and capture–recapture data
<code>secr-varyingeffort.pdf</code>	variable effort (usage) in SECR models

The web page <https://www.otago.ac.nz/density/> should be checked for news of bug fixes and new releases. New versions will be posted on CRAN, but there may be a delay of a few days. Help may be sought on the Density | `secr` forum at www.phidot.org; see also the FAQ there for DENSITY and **secr**. Another forum intended for both software issues and wider discussion is `secr`group. For information on changes in each version, type at the R prompt:

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

Defining models with the ‘model’ argument of `secr.fit`

By default, the parameters of SECR models are assumed to be constant. We specify more interesting, and often better-fitting, models with the ‘model’ argument of `secr.fit`. Here ‘models’ relates to variation in the parameters that may be explained by known factors and covariates. The explanation in `secr-models.pdf` may help. If you just want to know how to use models, read on.

Models 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.

Three real parameters are commonly modelled in **secr** 5.0; these are denoted ‘D’ (for density), ‘g0’ (or ‘lambda0’) and ‘sigma’. Only the last two 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 (`derivedCluster` etc.).

Here is a simple example of the model argument in use:

```
secr.fit(captdata, model = g0~t)
```

The real parameter g0 is no longer constant, but takes a unique value on each sampling occasion (t).

Other ‘real’ parameters appear in particular contexts. ‘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`). Some detection functions primarily model ‘exposure’ or the cumulative hazard of detection, rather than the probability of detection; these use the real parameter ‘lambda0’ in place of ‘g0’ (see `?detectfn`). ‘lambda0’ is also used with count detectors. A further ‘real’ parameter is the mixing proportion ‘pmix’, used in finite mixture models and hybrid mixture models (see `?hcov`).

Sometimes it is illuminating and efficient to parameterise the detection function using a function of the primary ‘real’ parameters described above. This gives rise to the surrogate ‘real’ parameters a0 and sigmak; see the vignette `secr-parameterisations.pdf` for details and references.

Detection parameters and density parameters are modelled separately, as we now describe.

Detection parameters

Effects on parameters of detection probability are specified via R formulae. The variable names used in formulae are either names for standard effects (Table 5) 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. See also the later section on modelling sex differences.

Table 5. Automatically generated predictor variables used in detection models

Variable	Description	Notes
g	group	individual covariates listed in <code>secr.fit</code> argument ‘groups’
t	time factor	one level for each occasion
T	time trend	linear trend over occasions on link scale
b	learned response	step change after first detection
B	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 occasion
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
ts	marking vs sighting	two levels (marking and sighting occasions)

Any name in a formula that is not a variable in Table 5 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, or named with the ‘timevaryingcov’ attribute of a traps object, using the first match (Table 6).

Table 6. Types of user-provided covariate for in detection models. The names of columns in the respective dataframes, and names of components in the ‘timevaryingcov’ attribute, may be used in model formulae

Covariate type	Data source	Notes
Individual	covariates(capthist)	conditional likelihood only
Time	timecov argument	
Detector	covariates(traps(capthist))	
Detector x Time	covariates(traps(capthist))	see ?timevaryingcov
Session	sessioncov argument	

The formula for any detection parameter (e.g., g_0 , λ_0 or σ) may be constant (~ 1 , the default) or some combination of terms in standard R formula notation (see ?formula). For example, $g_0 \sim b + T$ specifies a model with a learned response and a linear time trend in g_0 ; the effects are additive on the link scale. See Table 7 for other examples.

Table 7. Some examples of the ‘model’ argument in `secr.fit`

Formula	Effect
$g_0 \sim 1$	g_0 is constant across animals, occasions and detectors
$g_0 \sim b$	learned response affects g_0
<code>list($g_0 \sim b$, $\sigma \sim b$)</code>	learned response affects both g_0 and σ
$g_0 \sim h_2$	2-class finite mixture for heterogeneity in g_0
$g_0 \sim b + T$	learned response in g_0 combined with trend over occasions
$\sigma \sim g$	detection scale σ differs between groups
$\sigma \sim g * T$	group-specific trend in σ
$D \sim \text{cover}$	density varies with ‘cover’, a variable in covariates(mask)
<code>list($D \sim g$, $g_0 \sim g$)</code>	both density and g_0 differ between groups
$D \sim \text{session}$	session-specific density

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.

Inhomogeneous density models

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.

Regression splines are particularly effective for modelling spatial trend. For these and general guidance on fitting and displaying density surfaces, see the vignette `secr-densitysurfaces.pdf`.

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 `sim.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 mask; 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 the animal, and on the chosen detection function. For specifics, see the separate vignette on habitat masks `secr-habitatmasks.pdf` and the help for 'mask' and the various mask-related functions (`make.mask`, `mask.check`, `suggest.buffer`, and `esaPlot`). 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.

Miscellaneous topics

Modelling sex differences

There are many ways to model sex differences in `secr`. Here we sketch some possibilities, in order of usefulness (your mileage may vary).

1. Fit a hybrid mixture model as described in the online help (`?hcov`). This accommodates occasional missing values and estimates the sex ratio (`pmix`).
2. Use conditional likelihood (`CL = TRUE`) and include a categorical (factor) covariate in model formulae (e.g., $g_0 \sim \text{sex}$). To get sex-specific densities then specify `groups = "sex"` in `derived`.
3. Use full likelihood (`CL = FALSE`) and separate data for the two sexes as different sessions (most easily, by coding 'female' or 'male' in the first column of the capture file read with `read.caphist`). Then include a group term 'session' in relevant model formulae (e.g., $g_0 \sim \text{session}$).
4. Use full likelihood (`CL = FALSE`), define `groups = "sex"` or similar, and include a group term 'g' in relevant formulae (e.g., $g_0 \sim g$).

'CL' and 'groups' are arguments of `secr.fit`. Possibilities 1–4 should not be mixed for comparing AIC. Sex differences in home-range size (and hence sigma) may be mitigated by compensatory variation in g_0 or λ_0 (Efford and Mowat 2014).

Varying effort

The probability of observing an individual at a particular detector may depend directly on a known quantity such as how long the detector was exposed on a particular occasion. In the extreme, a detector may not have been operated. The terms 'effort' and 'usage' are used here interchangeably for variation in the duration

of exposure and similar known effects. Usage is an attribute of the detectors in a traps object (a traps x occasions matrix); it may be entered with the detector coordinates in a trap layout file or added later (see ?usage). Models fitted to data including a usage attribute will adjust automatically for varying usage across detectors and occasions. Usage may take any non-negative value. This simplifies the modelling of data aggregated over varying numbers of occasions or nearby sites.

See the separate document `secr-varyingeffort.pdf` and Efford et al. (2013) for more.

Mark-resight

Mark-resight data include sampling occasions on which previously marked animals were recorded, but new animals were not distinguished from each other. **secr** 5.0 provides a suite of spatial models for these data, as documented in `secr-markresight.pdf`. Two general classes of spatial mark-resight model are included: those in which the marking process is modelled (we call these spatial capture-mark-resight models), and those in which the process is not modelled and pre-marked animals are assumed to follow some distribution (e.g., uniform across a known area) (sighting-only or mark-resight models). Mark-resight models in **secr** 5.0 discard some spatial information in the unmarked sightings – information that is used in the models of Chandler and Royle (2013) and Sollmann et al. (2013). This results in some (probably small) loss of precision, and requires an adjustment for overdispersion to ensure confidence intervals have good coverage properties. The vignette `secr-markresight.pdf` should be consulted.

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 to sample possible spatial variation in density. **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 cluster³.

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.

A lacework design (Efford in prep.) is an alternative to a clustered design that is suitable when the region is intermediate size. Lacework designs may be constructed with `make.lacework`.

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`, `derivedMash` and the method `predict.secr` use ‘n.mash’ to adjust their output density, SE, and confidence limits.

Parallel processing

On processors with multiple cores it is possible to speed up computation by using cores in parallel. In **secr** 5.0 this happens automatically in `secr.fit` and a few other functions using the multi-threading paradigm of **RcppParallel** (Allaire et al. 2021). The number of threads may be set directly with the function `setNumThreads`, or via the ‘ncores’ argument of several functions.

Earlier versions of **secr** relied on parallel processing with the **parallel** package (invoked when the argument `ncores` was set greater than 1). The benefits of that form of parallel processing were variable (considerable with simulations in `sim.secr`, but otherwise unimpressive).

The functions `par.secr.fit`, `par.region.N` and `par.derived` allowed models to be fitted or analysed in parallel, one per core. The greater speed of `secr.fit` in **secr** 5.0 makes `par.secr.fit` redundant. All three

³Clusters are assumed to share the same geometry (number of detectors, within-cluster spacing etc.).

functions now appear to run faster with `ncores=1` than with `ncores>1`. They are deprecated and will be removed later in 2024. `list.secr.fit` replaces `par.secr.fit`.

Regression splines

The standard models for ‘real’ parameters in **secr** are linear on the link scale, much like a generalised linear model. Semi-parametric ‘regression spline’ smooths provide more flexibility. These are implemented in **secr** using a method suggested by Borchers and Kidney (2014): Simon Wood’s R package **mgcv** is used to parse `s()` and `te()` terms in model formulae and construct basis functions that are used like linear covariates within **secr**. Any ‘real’ parameter may be modelled with regression splines (D, lambda0, sigma, noneuc etc.). For details see the help page (`?smooths`) and the documentation for **mgcv**.

Non-Euclidean distances

‘Distance’ in SECR models usually, and by default, means the Euclidean distance $d = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}$. The observation model can be customised by replacing the Euclidean distance with one that ‘warps’ space in some ecologically meaningful way. There are innumerable ways to do this. Royle et al. (2013) envisioned an ‘ecological distance’ that is a function of landscape covariates. Redefining distance is a way to model spatial variation in the size of home ranges, and hence the spatial scale of movement σ ; Efford et al. (2016) use this to model inverse covariation between density and home range size. Distances measured along a linear habitat network such as a river system are also non-Euclidean (see package **seclinear**).

secr provides general tools for specifying and modelling non-Euclidean distance, via the `secr.fit` details component ‘`userdist`’. This may be a user-specified function or a pre-computed matrix. See `secr-noneuclidean.pdf` for a full explanation and examples.

References

- Allaire, J. J., Francois, R., Ushey, K., Vandenbrouck, G., Geelnard, M. and Intel (2021) `RcppParallel`: Parallel Programming Tools for ‘Rcpp’. R package version 5.1.4. <https://CRAN.R-project.org/package=RcppParallel>.
- Borchers, D. L., Buckland, S. T. and Zucchini, W. (2002) *Estimating animal abundance: closed populations*. Springer, London.
- Borchers, D. L. and Efford, M. G. (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* **64**, 377–385.
- Borchers, D. L. and Fewster, R. M. (2016) Spatial capture–recapture models. *Statistical Science* **31**, 219–232.
- Borchers, D. L. and Kidney, D. (2014) Flexible density surface estimation for spatially explicit capture–recapture surveys. Technical Report, University of St Andrews.
- Chandler, R. B. and Royle, J. A. (2013) Spatially explicit models for inference about density in unmarked or partially marked populations. *Annals of Applied Statistics* **7**, 936–954.
- Cooch, E. and White, G. (eds) (2014) *Program MARK: A Gentle Introduction*. 13th edition. Most recent edition available online at www.phidot.org/software/mark/docs/book/.
- Distiller, G. and Borchers, D. L. (2015) A spatially explicit capture–recapture estimator for single-catch traps. *Ecology and Evolution* **5**, 5075–5087.
- Eddelbuettel, D. and Francois, R. (2011) `Rcpp`: Seamless R and C++ Integration. *Journal of Statistical Software* **40**(8), 1–18. <https://www.jstatsoft.org/v40/i08/>.
- Efford, M. G. (2004) Density estimation in live-trapping studies. *Oikos* **106**, 598–610.
- Efford, M. G. (2011) Estimation of population density by spatially explicit capture–recapture analysis of data from area searches. *Ecology* **92**, 2202–2207.

- Efford, M. G. (2012) *DENSITY 5.0: software for spatially explicit capture–recapture*. Department of Mathematics and Statistics, University of Otago, Dunedin, New Zealand <https://www.otago.ac.nz/density>.
- Efford, M. G., Borchers D. L. and Byrom, A. E. (2009) Density estimation by spatially explicit capture–recapture: likelihood-based methods. In: D. L. Thomson, E. G. Cooch, M. J. Conroy (eds) *Modeling Demographic Processes in Marked Populations*. Springer. Pp 255–269.
- Efford, M. G., Borchers D. L. and Mowat, G. (2013) Varying effort in capture–recapture studies. *Methods in Ecology and Evolution* **4**, 629–636.
- Efford, M. G., Dawson, D. K. and Borchers, D. L. (2009) Population density estimated from locations of individuals on a passive detector array. *Ecology* **90**, 2676–2682.
- Efford, M. G., Dawson, D. K., Jhala, Y. V. and Qureshi, Q. (2016) Density-dependent home-range size revealed by spatially explicit capture-recapture. *Ecography* **39**, 676–688.
- Efford, M. G. and Fewster, R. M. (2013) Estimating population size by spatially explicit capture–recapture. *Oikos* **122**, 918–928.
- Efford, M. G. and Mowat, G. (2014) Compensatory heterogeneity in spatially explicit capture–recapture data. *Ecology* **95**, 1341–1348.
- Efford, M. G. and Schofield, M. R. (2020) A spatial open-population capture–recapture model. *Biometrics* **76**, 392–402.
- Huggins, R. M. (1989) On the statistical analysis of capture experiments. *Biometrika* **76**, 133–140.
- Laake, J. and Rexstad E. (2014) Appendix C. RMark - an alternative approach to building linear models in MARK. In: Cooch, E. and White, G. (eds) *Program MARK: A Gentle Introduction*. 13th edition. most recent edition available at www.phidot.org/software/mark/docs/book/.
- Lebreton, J.-D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67–118.
- Otis, D. L., Burnham, K. P., White, G. C. and Anderson, D. R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**.
- Royle, J. A., Chandler, R. B., Gazenski, K. D. and Graves, T. A. (2013) Spatial capture–recapture models for jointly estimating population density and landscape connectivity. *Ecology* **94** 287–294.
- Royle, J. A., Chandler, R. B., Sollmann, R. and Gardner, B. (2014) *Spatial capture–recapture*. Academic Press.
- Royle, J. A. and Gardner, B. (2011) Hierarchical spatial capture–recapture models for estimating density from trapping arrays. In: A.F. O’Connell, J.D. Nichols and K.U. Karanth (eds) *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, Tokyo. Pp. 163–190.
- Royle, J. A., Nichols, J. D., Karanth, K. U. and Gopalaswamy, A. M. (2009). A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* **46**, 118–127.
- Royle, J. A. and Young, K. V. (2008) A hierarchical model for spatial capture–recapture data. *Ecology* **89**, 2281–2289.
- Sollmann, R., Gardner, B., Parsons, A. W., Stocking, J. J., McClintock, B. T., Simons, T. R., Pollock, K. H. and O’Connell, A. F. (2013) A spatial mark–resight model augmented with telemetry data. *Ecology* **94**, 553–559.
- Stanley, T. R. and Burnham, K. P. (1999) A closure test for time-specific capture–recapture data. *Environmental and Ecological Statistics* **6**, 197–209.

Appendix 1. Core functions of secr

These are the core functions of **secr** 5.0 – the ones that you are most likely to use. S3 methods are marked with an asterisk.

Function	Purpose
<code>addCovariates</code>	add spatial covariates to traps or mask
<code>AIC*</code>	model selection, model weights
<code>covariates</code>	extract or replace covariates of traps, capthist or mask
<code>derived*</code>	compute density from conditional likelihood models
<code>make.mask</code>	construct habitat mask (= mesh)
<code>plot*</code>	plot capthist, traps or mask
<code>read.capthist</code>	input captures and trap layout from Density format, one call
<code>predict*</code>	compute ‘real’ parameters for arbitrary levels of predictor variables
<code>predictDsurface</code>	evaluate density surface at each point of a mask
<code>region.N*</code>	compute expected and realised population size in specified region
<code>secr.fit</code>	maximum likelihood fit; result is a fitted ‘secr’ object
<code>summary*</code>	summarise capthist, traps or mask
<code>traps</code>	extract or replace traps object in capthist

Appendix 2. Classified index to secr functions

Here is an index of **secr** functions classified by use (some minor functions are omitted). S3 methods are marked with an asterisk.

- Manipulate core objects
- Attributes of traps object
- Attributes of capthist object
- Data for each detection
- Operate on fitted model(s)
- Mask diagnostics
- Specialised graphics
- Convert or export data
- Miscellaneous

Function	Purpose
Manipulate data objects	
<code>addCovariates</code>	add spatial covariates to ‘traps’ or ‘mask’
<code>as.mask</code>	coerce ‘traps’ object to ‘mask’ for specialised plotting
<code>deleteMaskPoints</code>	edit ‘mask’
<code>discretize</code>	rasterize area-search capthist data
<code>head*</code>	first rows of ‘capthist’, ‘traps’ or ‘mask’
<code>join</code>	combine sessions of multi-session ‘capthist’ object
<code>make.grid</code>	construct detector array
<code>make.capthist</code>	form ‘capthist’ from ‘traps’ and detection data
<code>make.mask</code>	construct habitat mask (mesh)
<code>make.systematic</code>	construct clustered random systematic design
<code>make.lacework</code>	construct lacework random systematic design
<code>MS.capthist</code>	combine ‘capthist’ objects into one multi-session ‘capthist’
<code>plot*</code>	plot ‘capthist’, ‘traps’ or ‘mask’
<code>plotMaskEdge</code>	draw line around mask cells
<code>randomHabitat</code>	generates habitat mask with random landscape
<code>rbind*</code>	append ‘capthist’, ‘traps’, ‘popn’ or ‘mask’ objects
<code>read.capthist</code>	input captures and trap layout from Density format, one call
<code>read.traps</code>	input detector locations from text file
<code>reduce*</code>	aggregate detectors or occasions; change detector type
<code>sim.capthist</code>	simulate capture histories
<code>sightingPlot</code>	bubble plot of sightings in capthist object
<code>snip</code>	split transect(s) into equal sections
<code>split*</code>	split a single-session capthist or mask by various criteria
<code>subset*</code>	filter ‘capthist’, ‘traps’ or ‘mask’
<code>summary*</code>	summarise ‘capthist’, ‘traps’ or ‘mask’
<code>tail*</code>	last rows of ‘capthist’, ‘traps’ or ‘mask’
<code>trap.builder</code>	construct various complex designs
<code>verify*</code>	check ‘capthist’, ‘traps’ or ‘mask’ for internal consistency
Attributes of traps object	
<code>clusterID</code>	cluster identifier
<code>clustertrap</code>	detector number within cluster
<code>covariates*</code>	detector-level covariates
<code>detector*</code>	detector type (‘multi’, ‘proximity’ etc.)
<code>markocc</code>	vector distinguishing marking and sighting occasions
<code>polyID*</code>	polygon or transect identifier
<code>timevaryingcov</code>	name time-varying covariate(s)
<code>usage*</code>	occasion- and detector-specific effort

Function	Purpose
Attributes of capthist object	
addSightings	add sighting data to a 'proximity', 'count' or 'polygon' object
addTelemetry	add telemetry data to a 'proximity' or 'count' object
covariates*	individual-level covariates, including grouping factors
session*	session identifier(s)
signalmatrix	sound x microphone table
telemetryxy	coordinates of telemetry fixes
Tm	counts of marked animals that were not identified
traps*	embedded traps object(s)
Tu	counts of unmarked animals
Data for each detection	
alive	TRUE/FALSE
animalID	individual ID
clusterID	cluster identifier
clustertrap	detector number within cluster
noise	noise (signal detectors)
occasion	occasion
signal	signal strength (signal detectors)
signalframe	whole signal noise dataframe (rows = detections)
trap	detector
xy	detection coordinates (polygon and transect detectors)
Fit SECR model(s)	
list.secr.fit	fit several models and return secrlist object
secr.fit	maximum likelihood fit; result is a fitted <code>secr</code> object
Operate on fitted model(s)	
adjustVarD	apply \hat{c} to density SE and confidence intervals
AIC*	model selection, model weights
chat.nk	overdispersion of activity centres
coef*	'beta' parameters
collate	tabulate estimates from several models
confint*	profile likelihood confidence intervals
CVa, CVa0	CV of individual detection from fitted mixture model
derived*	density from conditional likelihood models
deviance*	model deviance
df.residual*	degrees of freedom for deviance
derivednj	variance from replicated sampling units
derivedCluster	variance from replicated sampling units
derivedExternal	variance from replicated sampling units
ellipse.secr	confidence ellipses for estimated parameters

Function	Purpose
<pre> esa'* effective sampling area by individual fxi* probability density of home-range centre LLsurface* compute likelihood surface and plot contours logLik* log-likelihood of fitted model LR.test likelihood-ratio test of two models MCgof* Monte Carlo goodness-of-fit after Choo et al. 2024 modelAverage* combine estimates using AIC or 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 region.N* expected and realised population size in specified region RSE extract precision (relative SE) of 'real' parameter estimates score.test model selection with score statistic using observed information secr.test Monte Carlo goodness-of-fit tests simulate* generate realisations of fitted model sim.secr parametric bootstrap vcov* variance-covariance matrix of 'beta' or 'real' parameters **Mask diagnostics** esaPlot cumulative plot esa or \hat{D} vs buffer width mask.check likelihood or estimates vs. buffer width and spacing [6pt] suggest.buffer find buffer width to keep bias within bounds **Specialised graphics** bufferContour concave and convex boundary strips fxTotal summed pdfs of home-range centre pdfs (use </pre>	<p>frequency distribution of detectors per animal</p>

Appendix 3. Datasets

See each help page for details e.g., ?deermouse. Code for model fitting is in Appendix 2 of secr-version4.pdf.
'blackbear'

Ursus americanus Tennessee Great Smoky Mountains 2003 DNA hair snag data of J. Laufenberg, F. van Manen and J. Clark; an earlier version was described by Settlage et al. (2008) *Journal of Wildlife Management* **72**.

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 published as a CAPTURE example by Otis et al. (1978) *Wildlife Monographs* **62**

ovenbird

Multi-year mist-netting study of ovenbirds *Seiurus aurocapilla* at a site in Maryland, USA.

ovensong

Acoustic detections of ovenbirds (Dawson & Efford *Journal of Applied Ecology* **46**, 1201–1209)

OVpossum

Brush-tail possum *Trichosurus vulpecula* live trapping in the Orongorongo Valley, Wellington, New Zealand 1996–1997 (Efford and Cowan In: *The Biology of Australian Possums and Gliders* Goldingay and Jackson eds. Pp. 471–483).

possum

Brush-tail 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. lineocellatum*) 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 Matakītaki Valley, South Island, New Zealand (Efford, Borchers and Byrom 2009).