## <span id="page-0-0"></span>Package: sra (via r-universe)

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Type Package

Title Selection Response Analysis

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Imports stats, stats4, graphics

URL <https://github.com/lerouzic/sra>

Description Artificial selection through selective breeding is an efficient way to induce changes in traits of interest in experimental populations. This package (sra) provides a set of tools to analyse artificial-selection response datasets. The data typically feature for several generations the average value of a trait in a population, the variance of the trait, the population size and the average value of the parents that were chosen to breed. Sra implements two families of models aiming at describing the dynamics of the genetic architecture of the trait during the selection response. The first family relies on purely descriptive (phenomenological) models, based on an autoregressive framework. The second family provides different mechanistic models, accounting e.g. for inbreeding, mutations, genetic and environmental canalization, or epistasis. The parameters underlying the dynamics of the time series are estimated by maximum likelihood. The sra package thus provides (i) a wrapper for the R functions mle() and optim() aiming at fitting in a convenient way a predetermined set of models, and (ii) some functions to plot and analyze the output of the models.

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Repository https://lerouzic.r-universe.dev RemoteUrl https://github.com/lerouzic/sra <span id="page-1-0"></span>RemoteRef HEAD

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## Contents



1. sra package *Selection Response Analysis: a* R *package*

#### Description

This package (sra) provides a set of tools to analyse artificial-selection response datasets. The data typically feature for several generations the average value of a trait in a population, the variance of the trait, the population size and the average value of the parents that were chosen to breed. sra implements two families of models aiming at describing the dynamics of the genetic architecture of the trait during the selection response. The first family relies on purely descriptive (phenomenological) models, based on an autoregressive framework. The second family provides different mechanistic models, accounting e.g.\ for inbreeding, mutations, genetic and environmental canalization, or epistasis. The parameters underlying the dynamics of the time series are estimated by maximum likelihood. The sra package thus provides (i) a wrapper for the R functions [mle](#page-0-0) and [optim](#page-0-0) aiming at fitting in a convenient way a predetermined set of models, and (ii) some functions to plot and analyze the output of the models.

## Details



Data set The user must provide (i) a vector containing the mean phenotype for all generations, (ii) a vector containing the phenoypic variance, (iii) a vector for the population sizes, (iv) a vector for the mean phenotype of the breeders, (v) (if available) a vector of the phenotypic variances among breeders. Several time series (e.g.\ several lines submitted to similar or different selection pressures) can be analyzed.

Phenomenological models The function [sraAutoreg](#page-3-1) fits an autoregressive model to the variance trends, and provides a description of the dynamics of the genetic architecture that is not based on

## <span id="page-2-0"></span>1. sra package 3

*a priori* biological mechanisms. The complexity of the model can be adjusted by adding extra autoregressive parameters.

Scaling The relevant scale for genetic architecture models is not necessarily the original measurement scale. Autoregressive models can be run from data e.g.\ on a log scale, but the package also provides two additional 'scales' that are specific to genetic architecture properties. [sraAutoregHerit](#page-3-1) fits the same models as [sraAutoreg](#page-3-1), but considering that the dynamics of environmental variance is constrained by the quantity known as "heritability" (ratio between additive and phenotypic variances). [sraAutoregEvolv](#page-3-1) proposes that both genetic and environmental variances are constrained by the mean of the population ("mean-scaled evolvability").

Mechanistic models Classical quantitative-genetics models are also provided. [sraCstvar](#page-6-1) implements a "constant-variance" model, [sraDrift](#page-6-1) considers the effects of inbreeding on the additive genetic variance, [sraMutation](#page-6-1) introduces some mutational variance, [sraCanalization](#page-6-1) illustrates the impact of a simple model of genetic and environmental canalization, [sraDirepistasis](#page-6-1) considers directional epistasis, and [sraSelection](#page-6-1) models the effect of unavoidable natural (stabilizing) selection competing with directional artificial selection.

Plotting and analysis All the models provide an objet of class srafit that can be plotted directly (see e.g. [plot.srafit](#page-10-1)).

## Author(s)

Arnaud Le Rouzic

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#### References

Le Rouzic, A., Houle, D., and Hansen, T.F. (2011) A modelling framework for the analysis of artificial selection-response time series. Genetics Research.

## Examples

########### Generating a dummy dataset ################

```
m <- c(12,11,12,14,18,17,19,22,20,19)
v <- c(53,47,97,155,150,102,65,144,179,126)
s <- c(15,14,14,17,21,20,22,25,24,NA)
n <- c(100,80,120,60,100,90,110,80,60,100)
```
########## Making a sra data set ####################### data <- sraData(phen.mean=m, phen.var=v, phen.sel=s, N=n)

#################### Data Analysis ####################

```
# Autoregressive models
autor <- sraAutoreg(data)
```

```
# AIC of the model:
AIC(autor)
```
# Maximum-likelihood estimates coef(autor)

```
autor.herit <- sraAutoregHerit(data)
autor.evolv <- sraAutoregEvolv(data)
# Mechanistic models
# Constant variance
cstvar <- sraCstvar(data)
# Inbreeding
drift <- sraDrift(data)
# Plotting
plot(drift)
plot(drift, var=TRUE)
```
2. Phenomenological models

*Descriptive models of artificial-selection responses: auto-regressive models*

#### <span id="page-3-1"></span>Description

The sraAutoreg functions are wrappers for the maximum-likelihood optimization function [mle](#page-0-0). They propose descriptive models for the dynamics of genetic architectures of different complexities based on an auto-regressive framework, additional parameters corresponding to different generation lags. The model can also be fit considering logatithmic, "heritability" and "evolvability" scales.

#### Usage

```
sraAutoreg(sradata, active = c(FALSE, TRUE, FALSE, FALSE),
start = NULL, fixed = NULL, negative.k = FALSE,
rand = 0, rep = 1, ...)
sraAutoregLog(sradata, active = c(FALSE, TRUE, FALSE, FALSE),
start = NULL, fixed = NULL, negative.k = FALSE,
rand = 0, rep = 1, ...)
sraAutoregHerit(sradata, active = c(FALSE, TRUE, FALSE, FALSE),
start = NULL, fixed = NULL, negative.k = FALSE,
rand = 0, rep = 1, ...sraAutoregEvolv(sradata, active = c(FALSE, TRUE, FALSE, FALSE),
start = NULL, fixed = NULL, negative.k = FALSE,
rand = 0, rep = 1, ...)
```
#### Arguments

sradata A data object generated by [sraData](#page-12-1).

active A vector of four booleans, corresponding to the active lags for both genetic and environmental variances (see Details). By default, only lag 1 is active, corresponding to an exponential change of the variances.

<span id="page-3-0"></span>

## <span id="page-4-0"></span>2. Phenomenological models 5



## Details

## Model

The following summarizes the models developed in Le Rouzic et al. 2010.

The mean of the population  $\mu$  changes according to the Lande equation (Lande and Arnold 1983):

$$
\mu(t+1) = \mu(t) + VarA(t) * \beta(t),
$$

where  $\beta(t)$  is the selection gradient at generation t.

The genetic architecture models predict the dynamics of a parameter P as:

$$
P(t+1) = k0 + k1 * P(t) + k2 * P(t-1) + k3 * P(t-2)
$$

Models with time lags > 3 could be easily implemented, but convergence issues increase with the number of parameters. The first time points are calculated as if  $P(t < 1) = P(1)$ , e.g.  $P(3) =$  $k0 + k1 * P(2) + k2 * P(1) + k3 * P(1).$ 

Each model considers the dynamics of two independent parameters, one related to the additive genetic variance  $(Var A)$ , one related to the residual (environmental) variance  $Var E$  (which actually also accounts for all non-additive genetic variance).

The default model sraAutoreg considers directly the dynamics of  $Var A$  (parameters: kA0, kA1, kA2, and kA3) and the dynamics of  $VarE$  (parameters kE0, kE1, kE2, and kE3).

The log scale turns a multiplicative trait into an additive one, and is particularly relevant for ratioscale traits (i.e. most quantitative traits such as size, fertility, etc). The original data is transformed assuming log-normality, and the likelihood is computed based on the log-normal density function.

<span id="page-5-0"></span>The "heritability" model sraAutoregHerit focuses on the dynamics of  $h^2\,=\,Var A/(Var A +$  $VarE$ ), described by the parameters kA0, kA1, kA2, and kA3, and considers that kE0, kE1, kE2, and kE3 describe the dynamics of the phenotypic variance  $VarP = VarA + VarE$ . Therefore,  $VarE$ is constrained both by the dynamics of  $VarP$  and the independent dynamics of  $h^2$ .

The "evolvability" model considers that kA0, kA1, kA2, and kA3 describe the dynamics of  $IA(t)$  =  $Var A(t)/(\mu(t)^2)$ , and kE0, kE1, kE2, and kE3 the dynamics of  $IE(t) = Var E(t)/(\mu(t)^2)$ .

#### Shortcut for active and inactive parameters

The user will often have to fit models of different complexity. This can be achieve by manipulating the active vector. c(FALSE,FALSE,FALSE,FALSE) corresponds to a constant-variance model (no dynamic parameter), c(TRUE,FALSE,FALSE,FALSE) to a case in which only kA0 and kE0 are active, c(TRUE,TRUE,FALSE,FALSE) to active parameters for lags 0 and 1 only, etc. The total number of parameters in the model will be  $3 + 2 * x$ , where x is the number of TRUE in the vector active.

To bypass the constrains of this shortcut, it is possible to specify the active and inactive parameters through the list of starting values. A combination such as active=c(TRUE,FALSE,TRUE,FALSE), start=list(kA1=0,kE3=NA), fixed=list(kE2=1) will lead to a model with 8 active parameters (mu0, varA0, varE0, kA0, kE0, kA1 (which starting value will be 0), kA2, and kE3 (which starting value, specified as NA, will be determined via the function [sraStartingvalues](#page-0-0). All other parameters are fixed.

## Parameterization

The models thus involve up to 11 parameters: three initial values ( $\mu(1)$ ,  $VarA(1)$  and  $VarE(1)$ ), four parameters to describe the dynamics of the additive variance (or relative variable such as  $IA$ or  $h^2$ ) (kA0, kA1, kA2, and kA3), and four parameters for the environmental variance (or IE, or  $h^2$ ): kE0, kE1, kE2, and kE3. To make numerical convergence more efficient, the following parameterization was implemented: parameters  $m\omega$ , logvarA $\omega$  and logvarE $\omega$  correspond to the estimates of the initial values of, respectively, the population mean, the logarithm of the additive variance, and the logarithm of the environmental variance. The parameters kA0 and kE0 are calculated as relative to the initial values of the dynamic variable, e.g. relativekA $\theta = k0A/Var A(1)$  (so that relativekA0 has the same unit and the same order of magnitude as kA1, kA2 and kA3).

#### Value

The functions return objects of class srafit, a list containing information about the model, the data, and the parameter estimates. Some standard R functions can be applied to the object, including AIC ([AIC.srafit](#page-9-1)), logLik ([logLik.srafit](#page-9-1)), vcov ([vcov.srafit](#page-9-1)), coef ([coef.srafit](#page-9-1)) confint ([confint.srafit](#page-9-1)), and plot ([plot.srafit](#page-10-1)).

#### Author(s)

Arnaud Le Rouzic

#### References

Le Rouzic, A., Houle, D., and Hansen, T.F. (2011) A modelling framework for the analysis of artificial selection-response time series. Genetics Research.

Lande, R., and Arnold, S. (1983) The measurement of selection on correlated characters. Evolution 37:1210-1226.

## <span id="page-6-0"></span>3. Mechanistic models 7

#### See Also

[sraCstvar](#page-6-1), [sraDrift](#page-6-1) and all other mechanistic models, [sraAutoregTsMinuslogL](#page-0-0) and [sraAutoregTimeseries](#page-0-0) for some details about the internal functions, [AIC.srafit](#page-9-1), [logLik.srafit](#page-9-1), [vcov.srafit](#page-9-1), [coef.srafit](#page-9-1), [confint.srafit](#page-9-1), [plot.srafit](#page-10-1) for the analysis of the results.

#### Examples

```
# Making the example reproducible
########### Generating a dummy dataset ################
m <- c(12,11,12,14,18,17,19,22,20,19)
v <- c(53,47,97,155,150,102,65,144,179,126)
s <- c(15,14,14,17,21,20,22,25,24,NA)
n <- c(100,80,120,60,100,90,110,80,60,100)
########## Making a sra data set #######################
data <- sraData(phen.mean=m, phen.var=v, phen.sel=s, N=n)
#################### Data Analysis ####################
# Autoregressive models
autor <- sraAutoreg(data)
# Details of the model:
AIC(autor)
coef(autor)
plot(autor)
plot(autor, var=TRUE)
# Alternative scales
autor.log <- sraAutoregLog(data)
autor.herit <- sraAutoregHerit(data)
autor.evolv <- sraAutoregEvolv(data)
# Changes in the complexity of the model:
autor0 <- sraAutoreg(data, active=c(TRUE,TRUE,FALSE,FALSE))
# In case of convergence issues
autor1 <- sraAutoreg(data, active=c(TRUE,TRUE,TRUE,TRUE), rep=2, rand=0.1)
```
3. Mechanistic models *Descriptive models of artificial-selection responses: quantitative genetics models*

## <span id="page-6-1"></span>Description

The sra functions for mechanistic model are wrappers for the maximum-likelihood optimization routine [mle](#page-0-0). They implement classical quantitative genetics models, fit them to artificial-selection time series, and provide estimates of e.g. the effective population size, the mutational variance, the strength of genetic / environmental canalization, the directionality and strength of epistasis, etc., given some assumptions about the properties of the genetic architecture.

#### Usage

sraCstvar(sradata, start=NULL, fixed=NULL, macroE=FALSE, Bulmer=TRUE, ...) sraDrift(sradata, start=NULL, fixed=NULL, macroE=FALSE, Bulmer=TRUE, ...) sraMutation(sradata, start=NULL, fixed=NULL, macroE=FALSE, Bulmer=TRUE, ...) sraCanalization(sradata, start=NULL, fixed=NULL, macroE=FALSE, Bulmer=TRUE, ...) sraCanalizationOpt(sradata, start=NULL, fixed=NULL, macroE=FALSE, Bulmer=TRUE, ...) sraSelection(sradata, start=NULL, fixed=NULL, macroE=FALSE, Bulmer=TRUE, ...) sraDirepistasis(sradata, start=NULL, fixed=NULL, macroE=FALSE, ...)

## Arguments



#### Details

All functions (except sraDirepistasis) rely on the same underlying model, and thus simply provide convenient shortcuts for different sets of parameters to fit.

mu0 is the initial phenotype of the population.

logvarA0 is the logarithm of the initial additive variance in the population.

logvarE0 is the logarithm of the initial environmental variance in the population.

logNe is the logarithm of the effective population size.

logn is the logarithm of the effective number of loci.

logvarM is the logarithm of the mutational variance.

kc and kg are the strength of environmental and genetic canalization, respectively.

o corresponds to the 'optimum' phenotype. When fixed and set to NA, o is identical to mu0. For convenience, the same optimum is used for environmental canalization, genetic canalization and natural stabilizing selection.

s corresponds to the strength of natural selection.

<span id="page-7-0"></span>

## <span id="page-8-0"></span>3. Mechanistic models 9

logvarepsilon is the logarithm of the variance of the epistatic coefficient ( $\varepsilon$ ). This parameter is fixed by default, since it is unlikely that realistic data sets contain enough information to estimate it properly.

The dynamic model that is fitted (except of the directional epistasis, detailed in the next paragraph) is:

$$
\mu(t+1) = \mu(t) + VarA(t) * (\beta(t) + s\delta(t))
$$
  
\n
$$
VarA(t+1) = VarM + VarA(t) * (1 - 1/(2 * N_e)) * e^{kg * (|\delta(t+1)| - |\delta(t)|)}
$$
  
\n
$$
VarE(t+1) = VarE(t) * e^{kc * |\delta(t)|}
$$

 $\mu(1)$ ,  $VarA(1)$  and  $varE(1)$  are parameters of the model,  $\beta(t)$  is the selection gradient, calculated for each generation from the data set, and  $\delta(t) = \mu(t) - o$ .

The directional epistasis model has its own setting:

$$
\mu(t+1) = \mu(t) + varA(t) * \beta(t)
$$

$$
VarA(t+1) = VarA(t) + 2 * \beta(t) * \varepsilon * VarA(t)^{2}
$$

$$
VarE(t+1) = VarE(1) + (\varepsilon^{2} + Var\varepsilon) * VarA(t)^{2}
$$

Where epsilon is a key parameter, representing the directionality of epistasis (Hansen and Wagner 2001, Carter et al. 2005). The properties of the likelihood function when epsilon varies makes numerical convergence tricky, and the function SRAdirepistasis actually performs two model fits: one for positive epsilons (the estimated parameter being logepsilon) and one for negative epsilons (estimating logminusepsilon). The likelihood of both models is then compared, and the best model is returned, providing either logepsilon or logminusepsilon. Although part of the model, the parameter logvarepsilon appeared to affect environmental variance only weakly, and its estimation is problematic in most cases.

These models are extensively described in le Rouzic et al 2010.

#### Value

The functions return objects of class srafit, a list containing information about the model, the data, and the parameter estimates. Some standard R functions can be applied to the object, including AIC ([AIC.srafit](#page-9-1)), logLik ([logLik.srafit](#page-9-1)), vcov ([vcov.srafit](#page-9-1)), coef ([coef.srafit](#page-9-1)) confint ([confint.srafit](#page-9-1)), and plot ([plot.srafit](#page-10-1)).

#### Author(s)

Arnaud Le Rouzic

#### References

Carter, A.J.R., Hermisson, J. and Hansen, T.F. (2005) The role of epistatic genetic interactions in the response to selection and the evolution of evolvability. Theor. Pop. Biol. 68, 179-196.

Hansen, T.F. and Wagner, G.P. (2001) Modelling genetic architecture: a multilinear theory of gene interaction. Theor. Pop. biol. 59, 61-86.

Le Rouzic, A., Houle, D., and Hansen, T.F. (2010) A modelling framework for the analysis of artificial selection-response time series. in prep.

### See Also

[sraAutoreg](#page-3-1), [sraAutoregHerit](#page-3-1) and [sraAutoregEvolv](#page-3-1) for phenomenological models, [sraAutoregTsMinuslogL](#page-0-0) and [sraAutoregTimeseries](#page-0-0) for some details about the internal functions, [AIC.srafit](#page-9-1), [logLik.srafit](#page-9-1),[vcov.srafit](#page-9-1), [coef.srafit](#page-9-1), [confint.srafit](#page-9-1), [plot.srafit](#page-10-1) for the analysis of the results.

## Examples

########### Generating a dummy dataset ################

```
m <- c(12,11,12,14,18,17,19,22,20,19)
v <- c(53,47,97,155,150,102,65,144,179,126)
s <- c(15,14,14,17,21,20,22,25,24,NA)
n <- c(100,80,120,60,100,90,110,80,60,100)
```
########## Making a sra data set ####################### data <- sraData(phen.mean=m, phen.var=v, phen.sel=s, N=n)

#################### Data Analysis ####################

```
cstvar <- sraCstvar(data)
drift <- sraDrift(data)
direpi <- sraDirepistasis(data)
```

```
# In case of convergence problems, better starting values can be provided:
direpi <- sraDirepistasis(data, start=list(mu0=10, logvarA0=log(20), logvarE0=NA),
fixed=list(logNe=log(50)))
```
plot(cstvar)

AIC(direpi)

4. Methods for srafit objects *Overloaded functions for "srafit" objects*

## <span id="page-9-1"></span>Description

The functions return the output expected from the corresponding R functions, applied to an object of class srafit.

#### Usage

```
## S3 method for class 'srafit'
logLik(object, ...)
## S3 method for class 'srafit'
AIC(object, ...)
## S3 method for class 'srafit'
coef(object, ...)
```
<span id="page-9-0"></span>

## <span id="page-10-0"></span>5. plot.srafit  $\frac{11}{11}$

```
## S3 method for class 'srafit'
confint(object, ...)
## S3 method for class 'srafit'
vcov(object, ...)
```
## Arguments



## Details

The confidence intervals are calculated from the estimate standard errors, and are thus different (less precise) from what would be calculated from the profile likelihood.

## See Also

[sraAutoreg](#page-3-1), [sraCstvar](#page-6-1) and other mechanistic models, [AIC](#page-0-0), [coef](#page-0-0), [logLik](#page-0-0), [confint](#page-0-0), [vcov](#page-0-0).

## Examples

m <- c(12,11,12,14,18,17,19,22,20,19) v <- c(53,47,97,155,150,102,65,144,179,126) s <- c(15,14,14,17,21,20,22,25,24,NA) n <- c(100,80,120,60,100,90,110,80,60,100) ########## Making a sra data set ####################### data <- sraData(phen.mean=m, phen.var=v, phen.sel=s, N=n) #################### Data Analysis #################### cstvar <- sraCstvar(data) AIC(cstvar) logLik(cstvar) coef(cstvar) confint(cstvar) vcov(cstvar)

########### Generating a dummy dataset ################

5. plot.srafit *Plotting "srafit" objects*

#### <span id="page-10-1"></span>Description

These functions plot in a nice way the content of objects of class srafit, the result of sra model fitting.

## <span id="page-11-0"></span>Usage

```
## S3 method for class 'srafit'
plot(x, series = levels(x$data$rep), resid = FALSE,
   variance = FALSE, ...sraPlotMean(srafit, series=levels(srafit$data$rep), legend=TRUE,
                 xlim=NULL, ylim=NULL, xlab=NULL, ylab=NULL, pch=1, ...)
sraPlotMeanResid(srafit, series=levels(srafit$data$rep))
sraPlotVar (srafit, series=levels(srafit$data$rep), legend=TRUE,
             xlim=NULL, ylim=NULL, xlab=NULL, ylab=NULL, pch=1, ...)
sraPlotVarResid (srafit, series=levels(srafit$data$rep))
sraPlotlegend(labels, estimates, AIC=NULL, confint=NULL,
                       location="topleft")
sraFormatlegend(names, values, AIC=NULL, ...)
```
## Arguments



## Details

The only function that should be used by the end user is plot.srafit.

<span id="page-12-0"></span>6. sraData  $13$ 

#### Author(s)

Arnaud Le Rouzic

## See Also

[sraAutoreg](#page-3-1), [sraCstvar](#page-6-1).

## Examples

```
m <- c(12,11,12,14,18,17,19,22,20,19)
v <- c(53,47,97,155,150,102,65,144,179,126)
s <- c(15,14,14,17,21,20,22,25,24,NA)
n <- c(100,80,120,60,100,90,110,80,60,100)
########## Making a sra data set #######################
data <- sraData(phen.mean=m, phen.var=v, phen.sel=s, N=n)
cstvar <- sraCstvar(data)
plot(cstvar)
plot(cstvar, xlim=c(3,9))
plot(cstvar, var=TRUE, ylab="This is a custom Y axis label")
plot(cstvar, resid=TRUE, legend=FALSE, main="Constant variance model fit")
```
########### Generating a dummy dataset ################

6. sraData *Generates an object of class "sradata", necessary to run the models provided by the sra package.*

## <span id="page-12-1"></span>Description

The data necessary to analyse selection response time series are, for each generation, (i) the mean phenotype of the population, (ii) the phenotypic variance, (iii) the mean of the breeders, and (iv) the population size. These data have to be grouped into an object of class "sradata", which can be provided to the sra analysis functions such as [sraAutoreg](#page-3-1) or [sraCstvar](#page-6-1).

#### Usage

```
sraData(phen.mean, phen.var, phen.sel, var.sel=NULL, N=NULL,
 gen=NULL, rep=NULL)
```
#### Arguments



<span id="page-13-0"></span>

## Details

If not provided, the default value for N is 100. Incorrect values for N will affect the likelihood value and the maximum-likelihood estimates.

gen will be assumed to vary from 1 to the maximum number of generations by default.

If more than one time series are provided, it is dangerous not to specify gen or rep. rep can be any unique identifier. For instance, fro two times series of 3 generations each, gen can be c(1,2,3,1,2,3) and rep can be c("up","up","up","down","down","down").

## Value

An object of class sradata.

## See Also

[sraAutoreg](#page-3-1), [sraCstvar](#page-6-1), and other mechanistic models, [sraAutoregTimeseries](#page-0-0).

## Examples

########### Generating a dummy dataset ################

```
m <- c(12,11,12,14,18,17,19,22,20,19)
v <- c(53,47,97,155,150,102,65,144,179,126)
s <- c(15,14,14,17,21,20,22,25,24,NA)
n <- c(100,80,120,60,100,90,110,80,60,100)
```

```
########## Making a sra data set #######################
data <- sraData(phen.mean=m, phen.var=v, phen.sel=s, N=n)
```
# <span id="page-14-0"></span>Index

∗ datagen 6. sraData, [13](#page-12-0) ∗ hplot 5. plot.srafit, [11](#page-10-0) ∗ methods 4. Methods for srafit objects, [10](#page-9-0) ∗ models 2. Phenomenological models, [4](#page-3-0) 3. Mechanistic models, [7](#page-6-0) 5. plot.srafit, [11](#page-10-0) ∗ nonlinear 2. Phenomenological models, [4](#page-3-0) 3. Mechanistic models, [7](#page-6-0) ∗ package 1. sra package, [2](#page-1-0) ∗ ts 2. Phenomenological models, [4](#page-3-0) 3. Mechanistic models, [7](#page-6-0) 1. sra package, [2](#page-1-0) 2. Phenomenological models, [4](#page-3-0) 3. Mechanistic models, [7](#page-6-0) 4. Methods for srafit objects, [10](#page-9-0) 5. plot.srafit, [11](#page-10-0) 6. sraData, [13](#page-12-0) AIC, *[11](#page-10-0)* AIC.srafit, *[6,](#page-5-0) [7](#page-6-0)*, *[9,](#page-8-0) [10](#page-9-0)* AIC.srafit *(*4. Methods for srafit objects*)*, [10](#page-9-0) coef, *[11](#page-10-0)* coef.srafit, *[6,](#page-5-0) [7](#page-6-0)*, *[9,](#page-8-0) [10](#page-9-0)* coef.srafit *(*4. Methods for srafit objects*)*, [10](#page-9-0) confint, *[11](#page-10-0)* confint.srafit, *[6,](#page-5-0) [7](#page-6-0)*, *[9,](#page-8-0) [10](#page-9-0)* confint.srafit *(*4. Methods for srafit objects*)*, [10](#page-9-0)

format, *[12](#page-11-0)*

legend, *[12](#page-11-0)* logLik, *[11](#page-10-0)* logLik.srafit, *[6,](#page-5-0) [7](#page-6-0)*, *[9,](#page-8-0) [10](#page-9-0)* logLik.srafit *(*4. Methods for srafit objects*)*, [10](#page-9-0) mle, *[2](#page-1-0)*, *[4,](#page-3-0) [5](#page-4-0)*, *[7,](#page-6-0) [8](#page-7-0)* optim, *[2](#page-1-0)*, *[5](#page-4-0)*, *[8](#page-7-0)* par, *[12](#page-11-0)* plot, *[12](#page-11-0)* plot.srafit, *[3](#page-2-0)*, *[6,](#page-5-0) [7](#page-6-0)*, *[9,](#page-8-0) [10](#page-9-0)* plot.srafit *(*5. plot.srafit*)*, [11](#page-10-0) sra *(*1. sra package*)*, [2](#page-1-0) sra-package *(*1. sra package*)*, [2](#page-1-0) sraAutoreg, *[2,](#page-1-0) [3](#page-2-0)*, *[10,](#page-9-0) [11](#page-10-0)*, *[13,](#page-12-0) [14](#page-13-0)* sraAutoreg *(*2. Phenomenological models*)*, [4](#page-3-0) sraAutoregEvolv, *[3](#page-2-0)*, *[10](#page-9-0)* sraAutoregEvolv *(*2. Phenomenological models*)*, [4](#page-3-0) sraAutoregHerit, *[3](#page-2-0)*, *[10](#page-9-0)* sraAutoregHerit *(*2. Phenomenological models*)*, [4](#page-3-0) sraAutoregLog *(*2. Phenomenological models*)*, [4](#page-3-0) sraAutoregTimeseries, *[7](#page-6-0)*, *[10](#page-9-0)*, *[14](#page-13-0)* sraAutoregTsMinuslogL, *[7](#page-6-0)*, *[10](#page-9-0)* sraCanalization, *[3](#page-2-0)* sraCanalization *(*3. Mechanistic models*)*, [7](#page-6-0) sraCanalizationOpt *(*3. Mechanistic models*)*, [7](#page-6-0) sraCstvar, *[3](#page-2-0)*, *[7](#page-6-0)*, *[11](#page-10-0)*, *[13,](#page-12-0) [14](#page-13-0)* sraCstvar *(*3. Mechanistic models*)*, [7](#page-6-0) sraData, *[4](#page-3-0)*, *[8](#page-7-0)* sraData *(*6. sraData*)*, [13](#page-12-0) sraDirepistasis, *[3](#page-2-0)*

```
sraDirepistasis
(3. Mechanistic
         models
)
,
7
sraDrift
,
3
,
7
sraDrift
(3. Mechanistic models
)
,
7
sraFormatlegend
(5. plot.srafit
)
, 11
sraMutation
,
3
sraMutation
(3. Mechanistic models
)
,
7
sraPlotlegend
(5. plot.srafit
)
, 11
sraPlotMean
(5. plot.srafit
)
, 11
sraPlotMeanResid
(5. plot.srafit
)
, 11
sraPlotVar
(5. plot.srafit
)
, 11
sraPlotVarResid
(5. plot.srafit
)
, 11
sraSelection
,
3
sraSelection
(3. Mechanistic models
)
,
7
sraStartingvalues
,
5
,
6
,
8
```

```
vcov
, 11
vcov.srafit
,
6,
7
,
9
, 10
vcov.srafit
(4. Methods for srafit
         objects
)
, 10
```