Package 'AlleleRetain'

July 21, 2025

Type Package

Title Allele Retention, Inbreeding, and Demography

Version 2.0.2

Depends R (>= 3.4.0)

Suggests pedigree

Date 2018-01-11

Author Emily L. Weiser

Maintainer Emily Weiser <emily.l.weiser@gmail.com>

Description Simulate the effect of management or demography on allele retention and inbreeding accumulation in bottlenecked populations of animals with overlapping generations.

License GPL (>= 2)

ZipData yes

URL https://sites.google.com/site/alleleretain/

NeedsCompilation no

Repository CRAN

Date/Publication 2018-01-11 19:29:41 UTC

Contents

---

agerepro.summary   *Summary of Average Reproductive Success by Age*

Description

average reproductive success, by age and sex, in the final year of the simulation by `aRetain`. Must be run after `aRetain` is run with `trackall = TRUE`.

Usage

```
agerepro.summary(adata, maxage, sex)
```

Arguments

`adata`	list of output from `aRetain`
`maxage`	value of MaxAge used in `aRetain`, or the maximum age of interest for the summary, whichever is smaller
`sex`	sex to summarize; "male" or "female"

Value

A matrix with one row for each age and seven columns:

`age`	age of each individual, from 0 to MaxAge
`alive.mean`	mean number of individuals that lived to this age
`alive.sd`	SD across replicates in the number of individuals that lived to this age
`matings.mean`	mean number of matings per individual at this age
`matings.sd`	SD among individuals in matings.mean
`offspring.mean`	mean number of offspring produced by individuals of this age
`offspring.sd`	SD among individuals in offspring.mean

Author(s)

Emily L. Weiser <emily.l.weiser@gmail.com>

References

Weiser, E.L., Grueber, C. E., and I. G. Jamieson. 2012. AlleleRetain: A program to assess management options for conserving allelic diversity in small, isolated populations. Molecular Ecology Resources 12:1161-1167.

AlleleRetain	*Allele Retention, Inbreeding, and Demography*

Description

Simulates the effect of management or demography on allele retention and inbreeding accumulation in bottlenecked populations of animals with overlapping generations.

Details

Typically, the user will run aRetain, then aRetain.summary to assess characteristics of the simulated population. indiv.summary, pedigree.summary (requires package **pedigree**), LRS.summary, and agerepro.summary will provide further output.

---

aRetain	*Allele Retention, Inbreeding, and Demography*

Description

Simulate the effect of management or demography on allele retention and inbreeding accumulation in bottlenecked populations of animals with overlapping generations.

Usage

```
aRetain(q0 = 0.05, sourceN = Inf,
startN = 20, startAge = "juvenile", startSR = 0.5, exactSSR= FALSE,
inisurv = c(1,1,1), addN = 0, addyrs = c(0),  addSR = 0.5, exactASR = FALSE,
migrN = 0, migrfreq = 1, migrSR = 0.5, exactMSR = FALSE, mpriority = FALSE,
removeL = FALSE, harvN = 0, harvAge = "all", harvyrs = 0, K = 100, Klag = 0,
KAdults = FALSE, reprolag = 0, mature = 1, matingSys = "monogamy",
matingLength = "seasonal", meanMLRS = 1, sdMLRS = 0, reproAgeM = c(1:200),
AgeOnMLRS = "age/age", nMatings = 1, retainBreeders = "male", MaxAge = 25,
SenesAge = 10, adsurvivalF = 0.80, adsurvivalM = 0.80, nonbrsurv = 0.80,
nonbrsurvK = 0.80, juvsurv = 0.80,  juvsurvK = 0.80, youngperF = 1.5,
SDypF = 0.25, ypF1 = 1, ypF1yr = 1, MAXypF = 2, MAXypFK = 2,
ypFsex = "female", youngSR = 0.5, trackall = TRUE, GeneCount = "adult",
nyears = 50, nrepl = 100, nreplprint = 10, printplots = FALSE)
```

Arguments

q0	frequency of rare allele in the source population (range 0-1)
sourceN	size of source population; must be > startN
startN	number of starters (or size of bottleneck); not all will become genetic founders; minimum 2

startAge	age class ("juvenile", "young adult", or "adult") of starters, supplemental. If "juvenile", all individuals added are assigned age 0; if "young adult", all are assigned age at maturity; if "adult", ages are selected randomly based on the proportion of individuals in the source population expected to be of each age (based on the survival rates and senescence specified below)
startSR	sex ratio (proportion male) of starters, supplementals, and migrants
exactSSR	logical: whether startSR gives the exact sex ratio of individuals released
inisurv	initial survival rate, as a proportion (range 0-1), of individuals released. Given as a vector, where the first value is for starters, the second is for additional releases, and third is for migrants. Annual mortality applies after this value is used. Defaults to 1 for all three groups.
addN	list of numbers of individuals to release in years soon after population establishment ("supplementals")
addyrs	list of years in which to release supplementals. Each year corresponds to the number of individuals in the same position in the addN list
addSR	sex ratio (proportion male) of supplementals; defaults to 0.5 (must be between 0 and 1). This can be either a single value, or a vector, with each element in the vector corresponding to each instance of supplementation (must be the same length as addN)
exactASR	whether addSR gives the exact sex ratio of individuals released (TRUE) or sexes are assigned randomly based on the probability given by addSR (FALSE); defaults to FALSE. This can be either a single value, or a vector, with each element in the vector corresponding to each instance of supplementation (must be the same length as addN)
migrN	number of migrants to add
migrfreq	interval (number of years) at which to add migrN migrants; must be between 1 and nyears, below
migrSR	sex ratio (proportion male) of supplementals; defaults to 0.5 (must be between 0 and 1)
exactMSR	whether addSR gives the exact sex ratio of individuals released (TRUE) or sexes are assigned randomly based on the probability given by migrSR (FALSE); defaults to FALSE
mpriority	logical: whether migrants are given priority over locally produced offspring to recruit into any available breeding vacancies
removeL	logical: whether to remove the corresponding number of locally produced adults to make room for migrants in the population; only necessary if retainBreeders = "both"/"female"/"male"; will only come into play when population is at K
harvN	number to be removed in each harvest year
harvAge	age of individuals to be harvested (as for 'startAge'). If not enough individuals of this age are available, the harvest quota (harvN) will not be filled
harvyrs	vector of years in which harvest occurs
K	carrying capacity (population ceiling)
Klag	number of years for which population is held at or below initial size (breeding still occurs); indicates a prolonged bottleneck

KAdults	logical: whether K counts only adults, or all individuals (subadults, nonbreeders, helpers)
reprolag	number of years after establishment for which no reproduction occurs
mature	average age (in years) at sexual maturity (first breeding)
matingSys	mating system: "monogamy", "polygyny", or "polygynandry"; to model a polyandrous system, set to "polygyny" and then input female values for the "male" parameters (and male values for the "female" parameters)
matingLength	"seasonal" or "lifelong"; determines whether individuals retain the same mate from year to year or divorce
meanMLRS	mean lifetime reproductive success (LRS), in terms of number of matings that produce young (NOT number of offspring) a male gets over his lifetime; including those that never reproduce. Each male will be assigned an individual average from a gamma distribution with this mean and sdMLRS (the shape of the gamma function = (meanMLRS^2)/(sdMLRS^2); scale = (sdMLRS^2)/meanMLRS; see help for R function "rgamma" for more information). The gamma distribution was chosen because of its flexibility in shape appropriate to polygynous mating systems (from strongly right-skewed to nearly symmetrical). The SD:mean ratio is more important than the magnitude of the mean. This individual mean indicates the male's "quality" and will be used to assess his chance of mating, relative to other males present, each year (does not translate directly into actual LRS experienced by that male). Not used if matingSys = "monogamy"
sdMLRS	among-male standard deviation in LRS; used with meanMLRS as described above
reproAgeM	list of ages at which males are able to mate successfully
AgeOnMLRS	expression describing the proportion of LRS achieved by a male at a particular age (for ages contained within reproAgeM), e.g. "-5.4 + 1.5*age - 0.08*age^2"; if there is no effect of age, use the default value of "age/age" (equals 1 so all ages will be assigned the same average, given by meanMLRS)
nMatings	number of matings per female each year; only used when matingSys = "polygynandry"; must be a whole number
retainBreeders	should established breeders retain their breeding status from year to year, and prevent young individuals from recruiting if the population is at K? Specify which sex should be retained: "none", "both", "male", or "female". Only used when matingSys = "monogamy." When "none", all new recruits are added to the breeding population; individuals are randomly removed from that pool to truncate the population at K (so new recruits may randomly replace established breeders). When adults will likely survive and prevent new individuals from recruiting, e.g. with territorial species, set this at one of the other values as appropriate for your species. When pairing off widowed or divorced individuals, those of the retained sex(es) that bred previously will be guaranteed a new mate (if available); non-retained adults will compete with new recruits to mate with available adults. If the population is at K, new recruits will only fill vacancies left by adults that died (they will not replace any surviving adults, including females when retainBreeders = "male" and vice versa; i.e. "both" functions the same as "male" and "female" in this part of the model)

MaxAge	maximum allowable lifespan (in years); can be Inf
SenesAge	age (in years) after which annual survival will be reduced by senescence. Through this age, adult survival values are set according to adsurvivalF and adsurvivalM (below). After this age, annual survival decreases linearly until MaxAge (at which it is 0): new survival = survival - (survival / (MaxAge - SenesAge)) * (age - SenesAge)
adsurvivalF	annual survival rate of adult females
adsurvivalM	annual survival rate of adult males
nonbrsurv	annual survival rate of nonbreeders (subadults or adults that have never reproduced)
nonbrsurvK	annual survival rate of nonbreeders when population is at K (used instead of nonbrsurv). If given, subadult survival probability in each year depends on density of the population at the beginning of that year, according to the Beverton-Holt function for density dependence in survival (as in Morris & Doak 2002, Quantitative Conservation Biology): S(E(t)) = S(0)/(1 + beta * E(t)), where S(E(t)) is survival rate at population density E in year t, S(0) is survival when density is near 0, beta is the decline in survival as density increases, and E(t) is population density at time t. "Density" is defined in our model as the proportion of K that has been filled, as there is no spatial information in the model. The model solves for beta according to the user-specified values for nonbrsurv (S(0)) and nonbrsurvK (S at carrying capacity, where E = 1), then uses beta and S(0) to calculate density-dependent survival probability in each year
juvsurv	first year survival (from the stage described by youngperF, below, to the beginning of the next breeding season) when population is below K
juvsurvK	first year survival when population is at K (used instead of juvsurv); juvenile survival is density-dependent as for nonbrsurvK
youngperF	average number of offspring produced per mating each year (averaged over all pairs in population). For a polyandrous female, this is the average number of offspring produced each time she mates with a male (each year): youngperF * nMatings = total average offspring per year. youngperF can be calculated for any reproductive stage (eggs, chicks, independent juveniles) as long as juvsurv indicates the proportion of individuals that survive from this stage to the beginning of the following breeding season
SDypF	among-individual standard deviation of youngperF, e.g. 0.50 or 2.
ypF1	where younger breeders have reduced reproductive rates, this can be used to define the reproductive success for first reproductive stage (length of that stage is determined by ypF1yr, below); given as a proportion of youngperF.
ypF1yr	age after which ypF1 changes to youngperF (e.g. 1 if ypF1 applies to one-year-olds only, or 5 if it applies for the first 5 years and then increases to youngperF from age 6 onward)
MAXypF	maximum annual number of offspring per individual (e.g. based on biological constraints such as clutch size/renesting)
MAXypFK	maximum annual number of offspring per individual when population is at K, if different from MAXypF

ypFsex	which member of a pair limits the reproductive output for the year, based on the biology of the species of interest; can be "male", "female", or "both" (the last will average the male's and female's values)
youngSR	proportion of offspring that are male
trackall	logical: whether to track all individuals from the population through the whole simulation; must be TRUE to use indiv.summary or pedigree.summary after running the simulation
GeneCount	which alleles to count as retained: those in the "adult" population only, or those in "all" individuals (including subadults and other nonbreeders)
nyears	number of years to run the simulation
nrepl	number of iterations (replicates) to run
nreplprint	interval (number of replicates) at which to print a message with the current system time. Allows the user to gauge model progress and to estimate time to completion
printplots	logical: whether to plot the population growth (number of individuals, as defined by KAdults, present each year) and allele frequency (in the pool defined by GeneCount) as they change over time (TRUE or FALSE). One line will be plotted for each replicate immediately after it runs. Can be used to immediately gauge the demographics of the population (e.g. if it will grow as expected); will slow down the simulation by ~ 10-20 percent. Defaults to FALSE.

Details

The user indicates the number of individuals released to establish the population (bottleneck size), along with their age class (adult or juvenile), sex ratio, and post-release survival rate. These individuals can be released all at once or gradually over a period of years. Released individuals are assumed to be unrelated and are randomly assigned genotypes (zero, one, or two copies of a hypothetical neutral allele) according to a user-specified frequency of the allele in the source population. The simulated population can be held at the initial size to simulate a prolonged bottleneck (while reproduction occurs) or the user can specify a post-release lag with no reproduction. Otherwise, released individuals mature and recruit according to user-specified parameters. Species with delayed sexual maturity are modeled by preventing subadults from breeding until a user-specified age. Adults are randomly sorted into monogamous or polygynous breeding pairs, which re-form for multiple matings within one season (in polygynandry systems), remain together seasonally (in monogamous or polygynous systems), or remain together lifelong (in monogamous systems) depending on user-specified settings. Reproduction occurs each year based on individual or population means (depending on settings for individual variation in reproductive output) for the number of offspring produced per pair per year, which can change with age of the parents. Sex is randomly assigned to each offspring according to the user-specified sex ratio for juveniles and offspring inherit alleles from their parents via Mendelian inheritance. When the simulated population reaches the specified carrying capacity, population growth ceases by either preventing recruitment of offspring or removing randomly selected individuals (as indicated by the user). When individuals are removed at random, the user can choose to give priority to remain in the population to established breeders and/or immigrants (if any). Annual survival of individuals is determined by user-specified probabilities for each age class, with optional sex-specific survival rates for adults. The user can choose to incorporate density dependence into juvenile and subadult/nonbreeder survival probabilities and/or to specify senescence effects in survival of adults beyond a certain age.

The model simulates immigration at regular user-specified intervals by adding more individuals from the original source population. Immigrants can be prioritized over locally produced individuals to recruit into breeding vacancies. This scenario may be realistic when most locally produced juveniles would emigrate, or when locally produced juveniles would be removed by managers (e.g. to contribute to other populations or to make room for immigrants). Emigration can be simulated in this model by reducing the survival value for the appropriate age class, assuming emigrants and their descendants do not return to the modeled population.

Frequency of the allele of interest in the simulated population is recorded after each year of the simulation. The proportion of iterations in which the allele is retained to the end of the specified time period is interpreted as the probability of retaining the allele in the population over that period. The model outputs a census of the simulated population (adults, subadults/nonbreeders, pairs, founders, and immigrants) each year, and a list of information for each individual in the simulated population. The census information can be averaged across replicates with aRetain.summary. An individual summary function (indiv.summary) can output pertinent information (e.g. proportion bred, average number that bred per generation) about individuals of each origin (founder, local, or immigrant) in the population. A pedigree summary function (pedigree.summary) can be used to describe accumulation of inbreeding in the population by calling R package **pedigree**.

See the AlleleRetain Model Guide (available as a PDF file with this installation, or from the model's website at https://sites.google.com/site/alleleretain/) for more details and an example.

Value

aRetain returns a list of sub-lists, with one sub-list for each replicate which contains two matrices: one that summarizes the population information for that replicate (one row for each year; columns = number of adults, number of breeding females, number of breeding males, number of copies of the rare allele, number of pairs, number of nonbreeders, number of founders remaining, number of migrants alive, mean age of breeding pairs), and one that gives pertinent information for all individuals in that replicate (one row for each individual; columns = ID, dam, sire, origin [1=starter, 2=supplemental, 3=local, 4=immigrant], birth year, number of years alive in the population, number of years bred, year added to population). The latter matrix includes all individuals if trackall = TRUE, or only those alive at the end of the simulation if trackall = FALSE. Run aRetain.summary, indiv.summary, and pedigree.summary to generate useful output from this information (averaged across replicates).

Author(s)

Emily L. Weiser <emily.l.weiser@gmail.com>

References

Weiser, E.L., Grueber, C. E., and I. G. Jamieson. 2012. AlleleRetain: A program to assess management options for conserving allelic diversity in small, isolated populations. Molecular Ecology Resources 12:1161-1167.

Examples

```
## Simulate rare allele with frequency 0.05 in source population.
## 20 individuals are translocated to establish a new population with carrying
## capacity = 100 individuals.  An additional 5 individuals are translocated
```

```
## once every 10 years as immigrants. Demographic parameter values are for a
## monogamous passerine bird species with a 5-yr average lifespan.  Only 30
## iterations are run so the confidence intervals will be wide.

## Not run:

aR.temp <- aRetain(q0 = 0.05, sourceN = 2000, startN = 20, startAge =
"adult", startSR = 0.5, exactSSR = FALSE, inisurv = 0.90, addN = 0, addyrs
= c(0),  migrN = 5, migrfreq = 10, mpriority = FALSE, removeL = FALSE, K =
100, KAdults = FALSE, mature = 1, matingSys = "monogamy", matingLength =
"seasonal", retainBreeders = "male", MaxAge = 16, SenesAge = 5, adsurvivalF =
0.77, adsurvivalM = 0.77, nonbrsurv = 0.70, nonbrsurvK = 0.40, juvsurv = 0.60,
juvsurvK = 0.30, youngperF = 2.85, SDypF = 1.25, MAXypF = 6, MAXypFK = 6,
ypFsex = "female", youngSR = 0.5, trackall = TRUE, GeneCount = "all", nyears =
10, nrepl = 20, nreplprint = 10)

aRetain.summary(aR.temp,  GeneCount = "all", alpha=0.05, dropextinct = TRUE)


## End(Not run)
```

---

aRetain.summary   *Summarize Demographics and Allele Retention from* aRetain

---

Description

Summarize pertinent information about the population simulated by aRetain.

Usage

```
aRetain.summary(adata, GeneCount, alpha=0.05, dropextinct = FALSE)
```

Arguments

adata	list of output from aRetain
GeneCount	"adult" or "all" as specified for aRetain
alpha	confidence level e.g. 0.05 for 95% intervals
dropextinct	logical: should simulated populations that decline to zero be omitted from the summary?

Value

A matrix in which the rows correspond to simulation years (0,...,nyears) and the columns are summary variables:

MeanN	mean number of adults

SEN	SE for # adults
MeanNNonbr	mean # of nonbreeders
MeanBrF	mean # of breeding females
SEBrF	SE for # of breeding females
MeanBrM	mean # of breeding males
SEBrM	SE for # of breeding males
MeanNFound	mean # of founders (starters and supplemental individuals) remaining
MeanNMigr	mean # of immigrants present
MeanAge	mean age of breeding adults (those that are actually paired that year)
P.extant	probability that the population is extant (proportion of simulations in which the population does not become extinct)
P.xLCL	lower bound of the confidence interval for P.extant
P.xUCL	upper bound of the confidence interval for P.extant
P.retain	probability that the rare allele is present in the population
P.LCL	lower bound of the confidence interval for P.retain
P.UCL	upper bound of the confidence interval for P.retain
A.Freq	frequency of the rare allele in the simulated population (in adults or in all individuals, as per GeneCount argument in aRetain)
A.SE	standard error for A.Freq

Author(s)

Emily L. Weiser <emily.l.weiser@gmail.com>

References

Weiser, E.L., Grueber, C. E., and I. G. Jamieson. 2012. AlleleRetain: A program to assess management options for conserving allelic diversity in small, isolated populations. Molecular Ecology Resources 12:1161-1167.

---

indiv.summary	*Summary of Individual Information*

Description

Summarize information for individuals of each origin (starters, supplementals, locals, immigrants) simulated by aRetain. Must be run after aRetain is run with trackall = TRUE.

Usage

```
indiv.summary(adata, genlength, alpha=0.05)
```

Arguments

`adata`	list of output from `aRetain`
`genlength`	mean age of simulated individuals (breeding pairs only), as returned by `census.summary` (use the MeanAge value where it stabilizes after recovering from any founder age effects)
`alpha`	confidence level e.g. 0.05 for 95% intervals

Value

A matrix with 4 rows, one for each origin (starter, supplemental, local, immigrant) and the columns are summary variables:

`n`	total number of individuals from each origin, summed within each replicate and then averaged across replicates
`pbreed`	probability of each individual breeding (proportion that bred)
`pbreed.LCL`	lower confidence limit for pbreed
`pbreed.UCL`	upper confidence limit for pbreed
`YrsBred`	mean # years bred per individual (including those that never bred)
`YrsBredBr`	mean # of years bred per individual (that bred at least once)
`lifespan`	mean lifespan in the population
`effectivegen`	mean # of individuals that bred each generation
`NMatings`	mean # of total lifetime matings, across individuals

Author(s)

Emily L. Weiser <emily.l.weiser@gmail.com>

References

Weiser, E.L., Grueber, C. E., and I. G. Jamieson. 2012. AlleleRetain: A program to assess management options for conserving allelic diversity in small, isolated populations. Molecular Ecology Resources 12:1161-1167.

LRS.summary	*Summary of Lifetime Reproductive Success*

Description

List of number of matings for each individual of the specified sex, over whole lifetime and all years, as simulated by `aRetain`. Must be run after `aRetain` is run with `trackall = TRUE`.

Usage

```
LRS.summary(adata, sex)
```

Arguments

adata	list of output from aRetain
sex	sex to summarize; "male" or "female"

Value

A matrix with one row for each individual and two columns:

ID	ID number of the individual. ID numbers are unique within each replicate, but will be repeated across replicates
NMatings	number of times the individual mated during its lifetime. The individual-level data is not expected to be useful, but can be used to calculate the mean or a histogram of mating success

Author(s)

Emily L. Weiser <emily.l.weiser@gmail.com>

References

Weiser, E.L., Grueber, C. E., and I. G. Jamieson. 2012. AlleleRetain: A program to assess management options for conserving allelic diversity in small, isolated populations. Molecular Ecology Resources 12:1161-1167.

---

pedigree.summary	*Pedigree Simulation and Summary*

Description

Summarizes inbreeding accumulation in the population simulated by aRetain. Must be run after aRetain is run with trackall = TRUE. Requires package **pedigree**.

Usage

```
pedigree.summary(adata)
```

Arguments

adata	list of output from aRetain

Value

A matrix in which the rows correspond to simulation years (0,...,nyears) and the columns are summary variables:

year	year of simulation
meanF	mean F, averaged across individuals and then across replicates
varF	inter-replicate variance in F
indivVarF	inter-individual variance of F, averaged across replicates

Author(s)

Emily L. Weiser <emily.l.weiser@gmail.com>

References

Weiser, E.L., Grueber, C. E., and I. G. Jamieson. 2012. AlleleRetain: A program to assess management options for conserving allelic diversity in small, isolated populations. Molecular Ecology Resources 12:1161-1167.

Index