

Supplementary information: Selective harvest focused on sexual signal traits can lead to extinction under directional environmental change.

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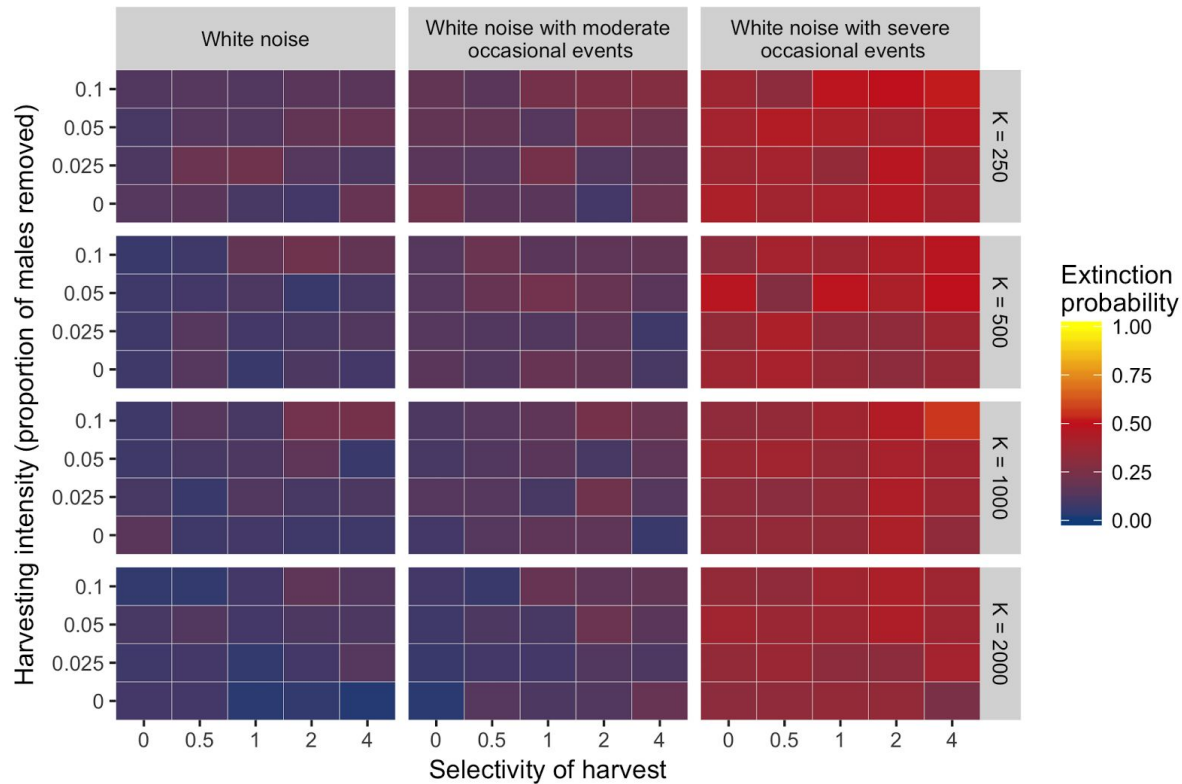
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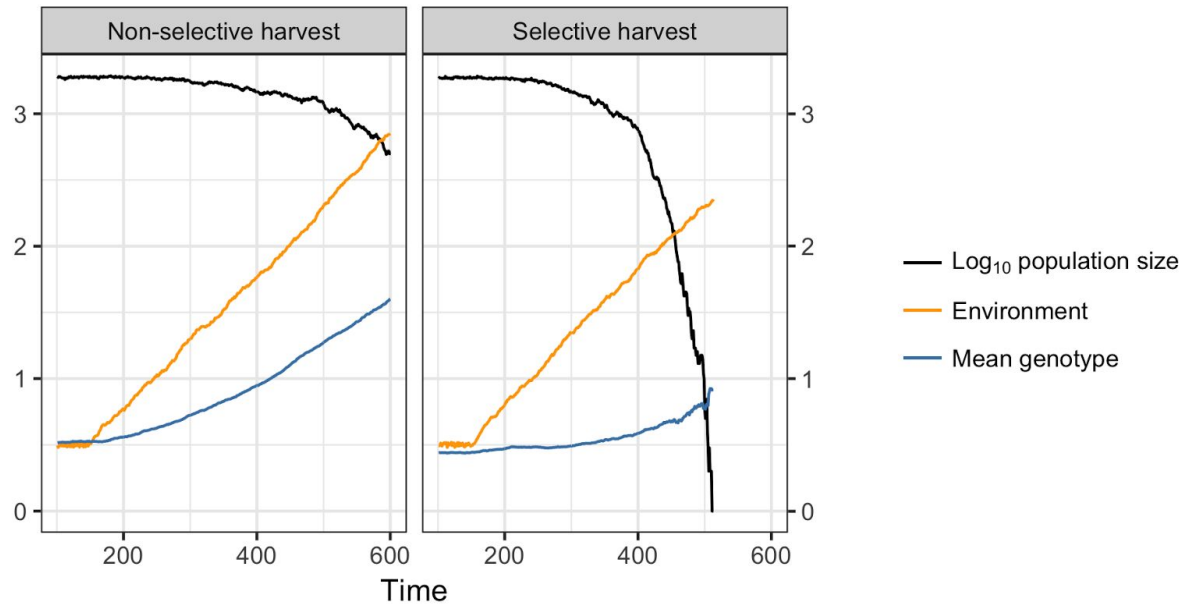
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S1 Further model exploration.



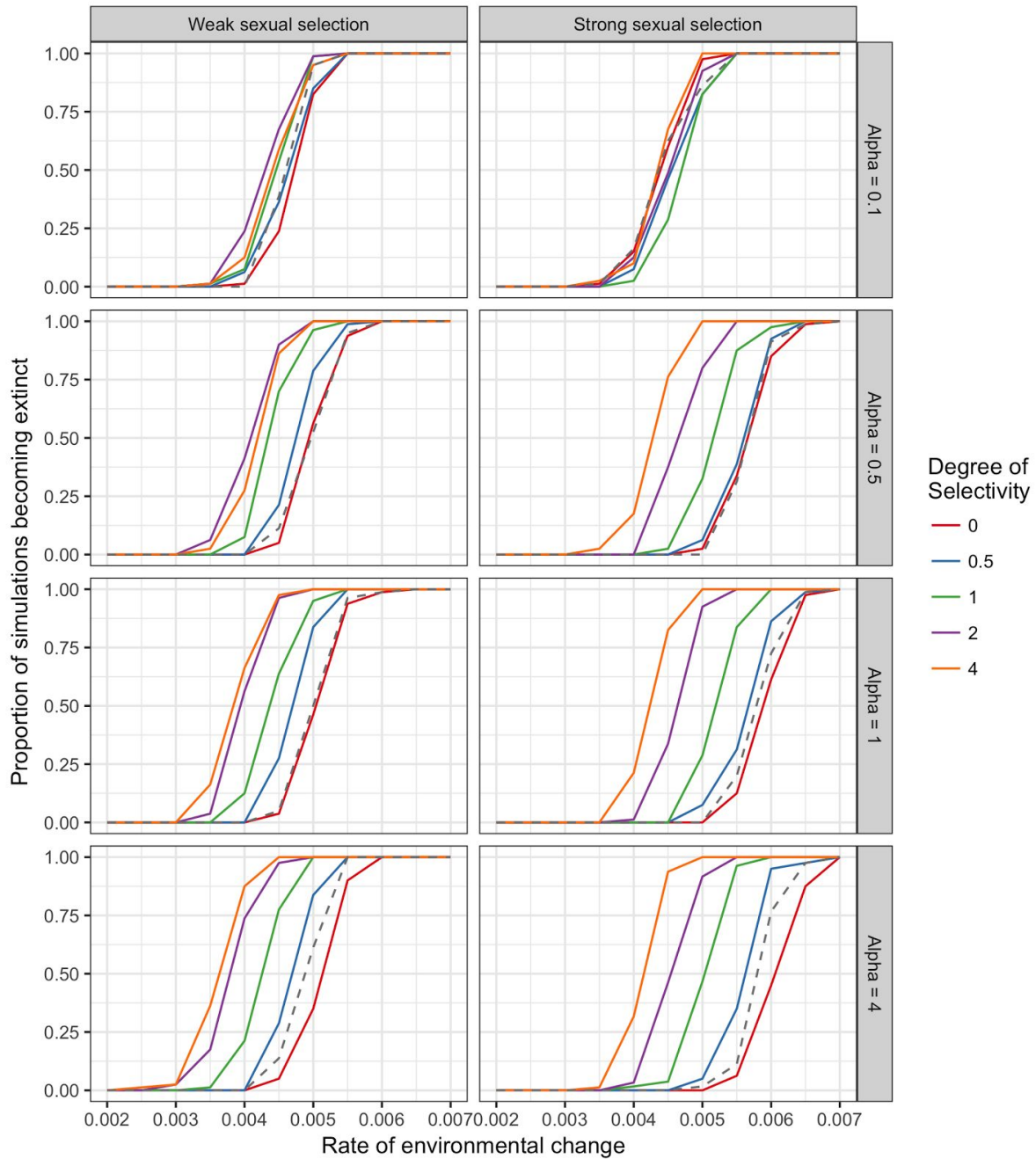
Supplementary Fig 1. Selective harvest of males does not increase extinction risk when the environment fluctuates randomly.

The figure shows extinction probabilities calculated from 80 model runs for three scenarios. The left hand column shows extinction probabilities for white noise fluctuations in the environment, whereby the environment alters every time step by a value drawn from a normal distribution with mean zero and standard deviation 0.05. The centre column shows extinction probabilities for a scenario as the left hand one but there is a 1/100 chance per time step of an event drawn from a normal distribution with mean zero and standard deviation 0.2. The right hand column is as the centre column but this time the occasional larger fluctuations are drawn from a normal distribution with mean zero and standard deviation 0.5. Larger populations are slightly more resilient but neither harvest strength nor selectivity affects the probability of extinction. All simulations run for 600 time steps with base fecundity = 5, strong sexual selection (strength of sexual selection = 5) and strong condition dependence (variable alpha = 4).



Supplementary Fig. 2. Comparison of simulation outputs for selectively and non-selectively harvested populations.

Both populations are set to the same set of parameter values (carrying capacity = 2000, maximum fecundity = 3, harvesting intensity = 0.2), and both experience directional change in the environment parameter after 150 time steps (NB the first 100 time steps are not shown for clarity). When harvest is non-selective the population mean genotype tracks the value of environment and the population persists, although in this case the amount of mismatch between genotype and environment does slowly increase and if this simulation were run for long enough the population would eventually become extinct. When harvest is selective, by contrast, the population is much less able to adapt to the changing environment and the value for mean genotype only responds a small amount to the new conditions. This leads to a rapidly increasing mismatch between genotype and environment, a swift decline in population size and extinction slightly after the 500th time step.



Supplementary Fig. 3. Effect of harvest selectivity, the strength of sexual selection and the degree of condition dependence at differing rates of environmental change.

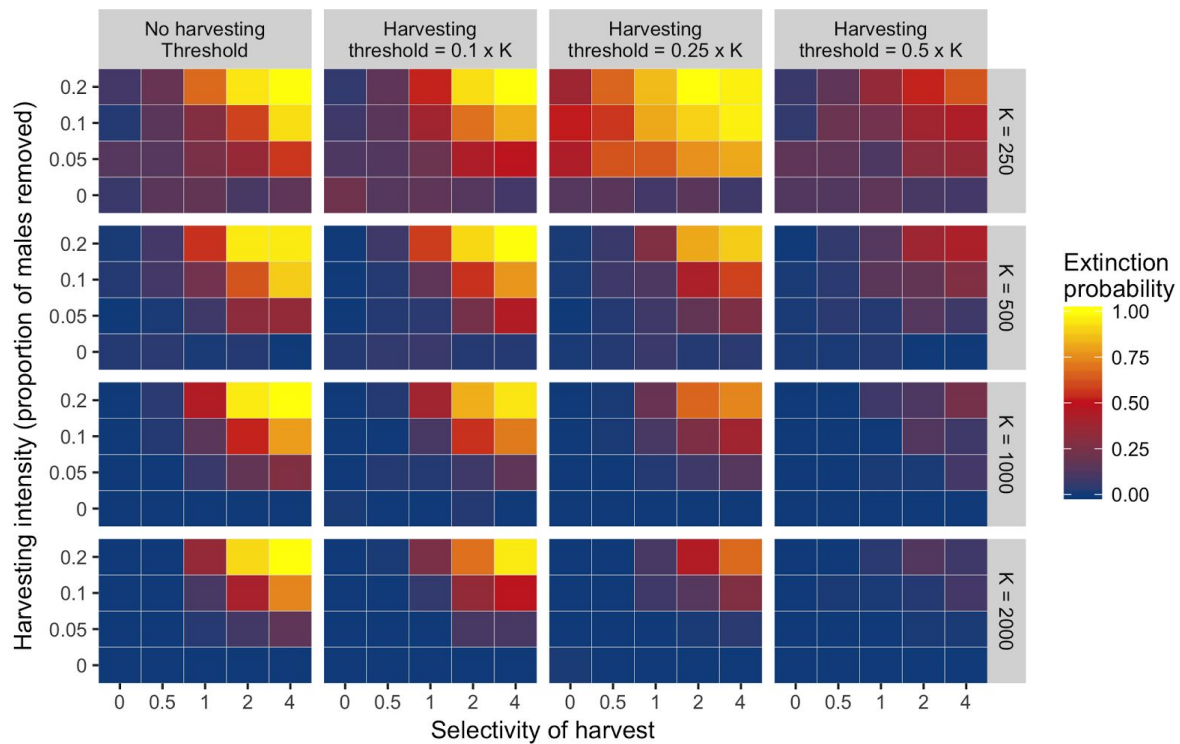
Each panel shows the proportion of simulations becoming extinct at differing rates of environmental change, for a range of different harvest selectivities (0 = random harvest of males, 4 = strong selection of males with the largest sexual ornaments for harvest). The dashed lines show the proportion of simulations becoming extinct when there is no harvest. Strong sexual selection means that each female evaluates five males before making a choice: weak sexual selection means that each female evaluates two males before choosing a mate. Alpha is the

parameter in the model relating the degree of mismatch with the environment to the degree of expression of the sexually selected trait. Alpha of 0.1 means that there is little connection between the male's fit to the environment and the expression of the sexual trait (mismatch explains about 15% of the variance in the sexual trait), and as alpha increases the connection becomes stronger: for alpha of 4 mismatch explains about 70% of the variance in sexual trait expression.

Strong sexual selection is associated with population persistence at a higher rate of environmental change – in other words, the Critical Rate of Environmental Change (CROEC) [1] above which the population becomes extinct increases with the strength of sexual selection. Selective harvesting reduces the CROEC in all cases except when $\alpha = 0.1$, and the effect of selective harvesting is somewhat stronger when sexual selection is strong. Condition dependence also affects the CROEC, with weaker condition dependence leading to population extinction at lower rates of environmental change. When condition dependence is sufficiently weak that there is little correlation between sexual trait expression and the male's fit to the environment, selective harvesting ceases to have an effect.

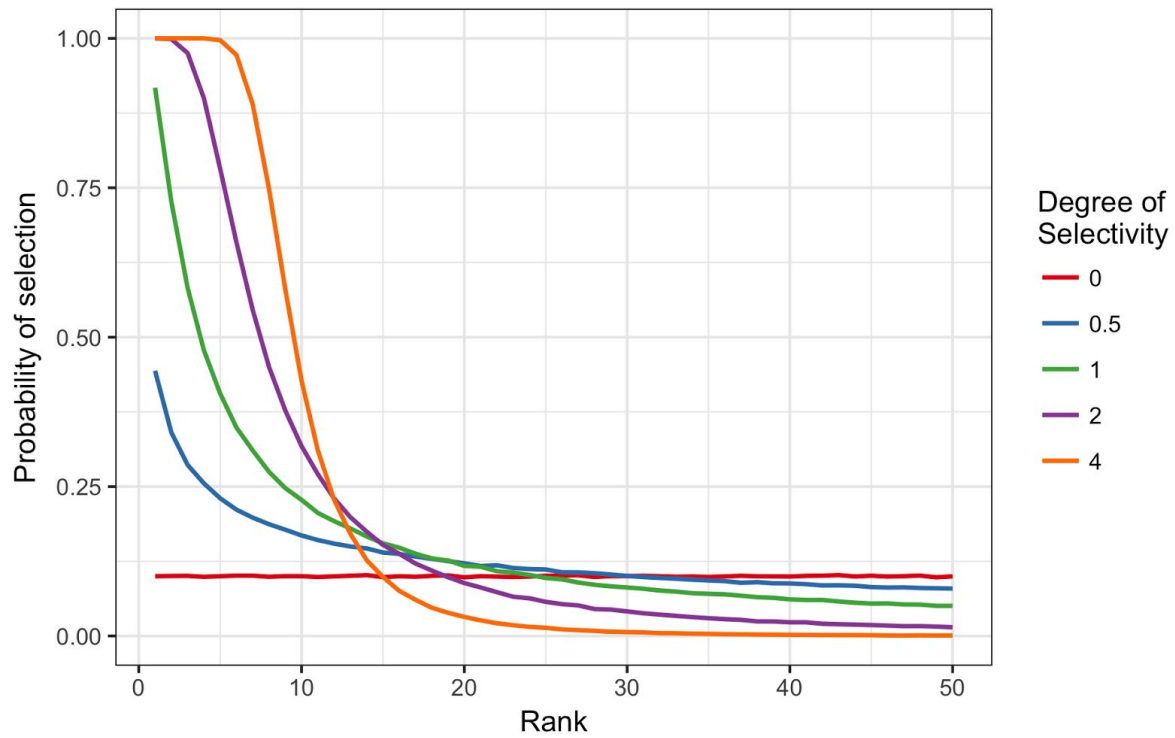
When sexual selection and/or condition dependence are strong, no harvest actually leads to a lower CROEC than does random harvest. As discussed in the main paper this is most likely an example of the 'hydra effect', whereby removal of some individuals from the population reduces competition and allows more recruitment, thereby increasing the number of new genotypes available for selection [2]. Why this does not occur when sexual selection and condition dependence are weak is not clear.

All simulations were replicated 80 times and were run for 600 time steps with the carrying capacity set to 1000 and the base fecundity to 3.



Supplementary Fig. 4. Effect of introducing a harvesting threshold on extinction probability.

The left hand column shows extinction probabilities when there is no harvesting threshold – note that this is the same as the second column from the left (fecundity = 3) for Fig. 2 in the main paper. The other three columns show extinction probabilities when there is a threshold below which no harvesting takes place, ranging from 10% to 50% of the carrying capacity. Note that this intervention is not especially effective and only causes substantial declines in extinction risk when the threshold is a large proportion of the carrying capacity. All extinction probabilities calculated from 80 replicate runs of the simulation, with base fecundity = 3, the rate of environmental change set to 0.005 per timestep, strong sexual selection (strength of sexual selection = 5) and strong condition dependence (variable alpha = 4).



Supplementary Fig. 5. Probability of harvest for individuals according to the ranked sizes of their secondary sexual traits.

Calculated from 100,000 simulations with 100 individuals each and 10 being selected. Note that when selectivity is set to zero the probability of harvest is independent of rank, when it is 4 (the highest value used in these simulations) harvest is highly selective towards the individuals with the greatest expression of secondary sexual traits.

S2 Detailed model description

Overview

Purpose

This Individual-Based Model (IBM) aims to simulate the evolution and dynamics of a population with a certain degree of sexual selection and condition dependence under specific environmental conditions, and to assess the effects of selective harvest of males depending on their expression of a secondary sexual trait.

State variables and scales

In the model a set of individuals is allowed to evolve in a changing environment. Both individuals and environment are defined by a set of features with values which can either be fixed or variable during simulation. These are listed with a brief description of each feature in table S1.

Process overview and scheduling

As the environment value changes every time step, many individual features must be recalculated. First, all individuals increase their age by one and those which are older than the age of maturity leave the immature subpopulation and enter either the female or male subpopulations. After that, individual environment is determined according to the new environmental value. Then, mismatch is recalculated as the squared difference between the new individual environment and each individual's genotype. Sexual display in mature males is recalculated taking into account the value of condition dependence and the new mismatch. Condition dependence determines how strongly the sexual display in males will correlate with its condition. Empirical approaches using measurable traits have shown that condition dependence is likely to be highly variable among species [3,4] and in time [5]. In this model condition dependence was a value correlating sexual trait in males with their fitness. As condition dependence is an abstract term, difficult to measure empirically [6], the values used here were those considered appropriate for the scale of variation within the model. Following recent studies that show that condition dependence does not necessarily increase as the display becomes more exaggerated [7], condition dependence is determined by a constant in this IBM. In the simulations described here males kept the same sexual display throughout their adult lives

because previous model exploration found that allowing annual regrowth made little difference to model outcomes [8].

After all individual features have been determined for a particular time step they are used to calculate each individual's death probability. Each individual is more or less likely to die depending on intraspecific competition, individuals' age and mismatch. Males' death probability also depends on their sexual display and its cost (Table S1). The effect of intraspecific competition increases as the population size approaches the carrying capacity. Younger and older individuals are more likely to die than mid age ones. As the mismatch between the organism's phenotype and the environment increases, so does the probability of death. Dead individuals are removed from the population. Following the removal of individuals by natural death individuals are removed by harvesting as described in the methods section of the main paper.

The surviving mature individuals then mate and reproduce. Each female chooses its mate from a subset of males based on the strength of its preference (females' sex trait), on the value of males' sexual display (males' sex trait) and on a random factor pulled from a normal distribution (mean = 0; SD = |median male's sex trait|/10) depending on the median sexual display in the population. The size of the pool of males from which each female chooses a mate is set by the population factor strength of sexual selection (Table S1). If this is set to 1, all matings are random and sexual selection is not acting, and as the pool of males becomes larger so the amount of reproductive skew in the system will increase, leading to stronger sexual selection. Females only mate with a single male, but males can mate with several females. This IBM thus excludes polyandry, which is likely to generate a number of trade-offs which are not yet well understood [9].

Once a female has chosen a mate they reproduce and generate new individuals. The number of offspring per female depends on the population factor fecundity (Table S1) and on the individual mismatch. The birth of each new individual is a probabilistic event which depends on birth probability (Table S1) and on intraspecific competition. All females mate but not all of them necessarily reproduce.

The genotype and sexual genotype of new individuals is defined depending on the same features in parents in addition of a random factor pulled from a normal distribution (mean = 0; SD = 0.005) which accounts for genetic variance between generations. Sexual genotype and genotype vary to the same extent and independently from each other. Therefore the model does not take into account direct genetic correlation between condition and display, but it assumes that the variance is the same [6]. The age of new individuals is set to 0. The rest of features are defined as in the initial population (Table S1).

Once new individuals have been generated and added to the population the environmental value is changed according to the environmental variability feature. If the feature is set to "Random",

the environmental value varies unpredictably, causing either a small or a sudden change in the environment every time step, being the former more frequent (probability of 0.99) than the latter (probability of 0.01). “Directional” environmental variation generates a stable environment during the first quarter of the simulation time and then the environmental value changes in the same direction every time step.

Table S1. List of the features defining the entities of the model. If environmental and population features are fixed, they remain the same during the whole simulation. Otherwise they change every time step. Individual features which are fixed remain the same during all individual’s life, whereas variable features change every time step. Alive status is an exception to this as it only changes once, when the individual dies. Initial values of environmental and population features affect the whole simulation. Initial values for individual features are only those of the initial population and will change for each new individual.

| Features | Fixed | Initial Values | Description |
|------------------------------------|-------|---|---|
| Environmental features | | | |
| Carrying Capacity | Yes | 250, 500, 1000 or 2000 | Maximum number of individuals that can coexist at one time |
| Environmental value (<i>env</i>) | No | A random number drawn from a normal distribution with mean 1 and standard deviation 0.5 | State of the environment at a given time step |
| Environmental variation | Yes | Random or directional | The type of environmental change |
| Rate of environmental change | Yes | 0.001, 0.002, 0.003, 0.0035, 0.004, 0.0045, 0.005, 0.0055, 0.006 | Amount by which <i>env</i> changes each generation after the 100 th if environmental variation is directional |
| Population features | | | |
| Age at maturity | Yes | 2 | The age at which an individual is able to reproduce |
| Fecundity | Yes | 2, 3, 4 or 5 | Maximum number of offspring that a female can produce |
| Strength of sexual selection | Yes | 5 or 2 | Number of males from whom a female selects a mate |
| Condition dependence (<i>CD</i>) | Yes | 4, 2, 1, 0.5 or 0.1 | How strongly male condition affects display |
| Female preference (<i>pref</i>) | Yes | 10 | Strength of female preference when choosing a mate |
| Cost of sexual display | Yes | 5 | How expression of secondary sexual traits affects lifespan in males |
| Timing of sexual display | Yes | Once only in the present example | Whether secondary sexual traits are grown once or every <i>timestep</i> . |
| Individual features | | | |
| Life status | No | 1 | Whether an individual is alive (1) or dead (0) |
| Sex | Yes | Male or female, assigned randomly | Sex of each individual. |
| Genotype | Yes | A number drawn from a normal distribution with mean <i>env</i> and standard deviation 0.75 | Genotype determining the individual’s fit to the environment and therefore its condition |
| Sexual genotype | Yes | A number drawn from a uniform distribution with minimum 1 and maximum 1.7* | Genotype determining the degree of expression of the secondary sexual trait in males, and the degree of preference in females |
| Individual environment | No | A number drawn from a normal distribution with mean <i>env</i> and standard deviation 0.2 | The environment as experienced by each individual |
| Mismatch | No | (Genotype – Individual environment) ² | Measure of how well adapted an individual is to its environment. |
| Sexual trait | No | Males: Sexual genotype / (1 + (Mismatch x <i>CD</i>)) Females: Sexual genotype + <i>pref</i> / (1 + <i>pref</i>) | In males: expression of the secondary sexual display trait In females: strength of preference |
| Age | No | An integer drawn from a uniform distribution with minimum 1 and maximum 10. | Age for each individual |
| Birth probability | No | 0.5 | Baseline birth probability |
| Death probability | No | 0.08 | Baseline death probability |
| Harvesting features | | | |
| Nature of harvest | Yes | Both sexes or males only. | Whether harvest is random across adults of both sexes or whether only adult males are targeted |
| Harvest selectivity | Yes | 0, 0.5, 1, 2 or 4 | If harvesting is male-only, how selective the harvest is (0 = random harvest, 4 = very selective, Fig. S1). |

Design concepts

Adaptation

Adaptation is driven by the feature genotype and its interaction with individual environment. Adaptation affects the survival of all individuals, the sexual display exaggeration in males and fertility in females. Since genotype is a fixed feature for an individual, adaptation does not occur at individual level but rather at population scale.

Fitness

In this IBM fitness is represented by mismatch. This feature measures how fitted a given genotype is for its environment (Table S1). When an individual's mismatch is 0, this individual is at its fitness peak.

Sensing

Individuals interact with their individual environment through their genotype. Individual environment value accounts for the variation of individual response to environment not relying on purely genetic aspects such as micro-climates and phenotypic effects. The closer the genotype of an individual is to its individual environment, the lower the mismatch.

Interaction

Individuals only interact directly during mating, but other indirect interactions arise as a result of the dynamics of the model. Indirect intralocus sexual conflict arises since sexual genotype defines both preference in females and sexual display in males. Preference has no cost in females, whereas sexual display is costly for males. Although female preference in nature is believed to have a cost [10], this was not taken into account since cost of preference does not increase with exaggeration of sexual display, as happens in males [5]. Cost of preference may play an important role only when exaggerated displays are generated [11], but the point of this study is to test the effects of sexual selection in populations in which it is already established. Indirect intraspecific competition is driven by the carrying capacity. The different values for carrying capacity (Table S1) are higher than in our previous study [8] because we wished to explore the effects of selective harvest on larger populations which are not necessarily at risk of extinction otherwise. The inclusion of these larger populations required considerable time and processing power, hence the reduced number of parameter combinations which we explored by comparison with the previous study. As for fecundity, the values used here were those considered realistic given the low values assessed for carrying capacity.

Initialization

The initial population consisted of 100 individuals, with its features defined as shown in Table S1. This was maintained for all simulations.

Input

The initial values of some key factors were changed among simulations. See Table S1 for more details. Each simulation lasted for 600 time steps unless the population went extinct before the simulation finished.

Submodels

The mathematical skeleton of all the processes described in the section Overview and scheduling are described in Table S2.

Simulations

Simulations were run on either a Linux workstation with 32GB RAM and an 8-core Intel i7 processor, or on the QMUL High Performance Cluster Apocrita (<http://docs.hpc.qmul.ac.uk/>). Parallelisation was managed using the R packages `parallel` [12], `DoMC` [13] and `foreach` [14]). 80 replicates of each parameter combination were run. R 3.4.0 was used in all cases.

Table S2 (next page). List of processes and subprocesses taking place in each simulation with their mathematical definition, timing and a brief description. Factors in equations: **U(X,Y)**: a random number between X and Y; **d**: baseline death probability; **K**: carrying capacity; **Population**: Total number of individuals at a given time step; **Mismatch**: Individual feature *mismatch*; **Age**: Individual feature age; **Cost**: Population feature cost; **Sexual display**: Individual feature sex trait in mature males; **Preference**: Individual feature sex trait in mature females; **N(X,Y)**: A random normally distributed number with mean X and standard deviation Y; **Median sexual display**: Median of the sexual display of all mature males for a given time step; **Fecundity**: The population feature fecundity; **Mother and father genotype** and **sexual genotype**: The individual features *genotype* and *sexual genotype* of the parents of a new individual. **Factor** and **Factor2**: A random number between 0 and 1; **time**: the number of time steps that the simulation will last; **Initial environment**: The environmental feature *environment* set at the beginning of the simulation; **Current environment**: The environmental feature *environment* at a given time step.

| Process | Subprocess | Formula | Frequency | Effect |
|----------------------|-------------------------------------|--|--------------------------------------|---|
| Death | In females and immature individuals | $U_{(0,1)} \leq d \cdot \left(\frac{K}{Population} + Mismatch + [(0.154 \cdot age)^2 - (0.169 \cdot age) + 0.46] \right)$ | Every female and immature individual | The right side of the inequality is the probability of death. If the inequality is true, the individual dies. |
| | In mature males | $U_{(0,1)} \leq d \cdot \left(\frac{K}{Population} + Mismatch + [(0.154 \cdot age)^2 - (0.169 \cdot age) + 0.46] + cost \cdot sexualdisplay \right)$ | Every mature male | As above but with an extra mortality cost from sexual display |
| Mating | Male attractiveness | $\left(sexualdisplay \cdot preference \right) + N \left(0,1 \frac{Mediansexualdisplay-1}{10} \right)$ | Every mature female | Higher values give males who are more attractive |
| Reproduction | Offspring per female | $Fecundity - Mismatch $ | Every mature female | The lower the fitness (higher mismatch), the lower the fecundity. |
| | Birth | $U_{(0,1)} \leq b \cdot \left(1 - \frac{Population}{K} \right)$ | Every new offspring | The right hand side of the inequality is the probability of birth. If the inequality is true a new individual is born |
| | Sexual genotype | $\frac{Mother'ssexualgenotype + Father'ssexualgenotype}{2} + N(0,0,05)$ | Every new born individual | Generates a new sexual genotype from the parents' values plus some random variation |
| Environmental change | Genotype (environmental) | $\frac{Mother'sgenotype + Father'sgenotype}{2} + N(0,0,05)$ | Every new born individual | Generates a new genotype from the parents' values plus some random variation |
| | Random | Normal change: $Current\ environmental\ value + N(0,random.sd1)$ P (Normal change = 0.99) Sudden change: $Current\ environmental\ value + N(0,random.sd2)$ P (Sudden change = 0.01) | Every time step | The environment changes at random, usually with small increments but with a small chance of a large change |
| Harvest | Directional | $If\ time\ step < \frac{time}{4} \quad Current\ environmental\ value + U(-0,02,0,02)$ $If\ time\ step \geq \frac{time}{4} \quad Current\ environmental\ value + directional\ rate$ | Every time step | After a quarter of the model's run time, the environment increases by a set increment every time step |
| | Both sexes: number removed | $Mature\ population \cdot harvest\ intensity$ | All mature individuals | This calculates the number of individuals who are removed during harvest if both sexes are to be harvested |
| | Male only: number removed | $Mature\ males \cdot harvest\ intensity$ | All mature males | This calculates the number of males who are removed during harvest if males only are to be harvested |
| | Male only: weighting | $weight_i = \left(\frac{1}{rank_i^{Selectivity}} \right) / \sum_{p=1}^{Males} rank_p$ | All mature males | This calculates the weighting to be used in male-only harvests. All mature males are ranked on the basis of their <i>sex trail</i> and the weighting calculated on the basis of this and the degree of <i>Selectivity</i> in the model. |

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14. Revolution Analytics, Weston S. 2015 foreach: Provides Foreach Looping Construct for R.

S3 Model Code

```
#####
```

```
#####
```

```
# Code for model of the effect of harvesting on sexually selected animals under random  
or directional environmental change, as detailed in Knell, R.J. and Martínez Ruiz, C.,  
Selective harvests can lead to extinction under directional environmental change
```

```
# Contact details: Rob Knell, School of Biological and Chemical Sciences, Queen Mary  
University of London, London E1 4NS, UK. email r.knell@qmul.ac.uk
```

```
#####
```

```
#####
```

```
# The model is coded as a function called "simulation_SS". To run it, just paste the  
entire text file into the R console, press enter and then type simulation_SS(). The  
arguments to the function can be used to change the model parameters, so  
simulation_SS(K = 500) will run the model for a carrying capacity of 500. All the model  
arguments are detailed below.
```

```
# This code is distributed under a creative commons attribution 4.0 international licence.  
You are free to share and adapt the code for both commercial and non-commercial  
purposes so long as appropriate attribution is made. See  
http://creativecommons.org/licenses/by/4.0/ for more details.
```

```
#Model parameters :
```


#b: probability of birth
#d: probability of death
#K: carrying capacity
#N0: starting number of individuals
#t: time of simulation
#e: environment
#O: Number of maximum offspring per female
#l: Age of maturity
#fem.sel: Nb of males selected per female. Accounts for the strength of sexual selection (if 'fem.sel=1', no sexual selection)
#alpha: How strongly environment scales with sexual trait in males. Accounts for condition dependence in the trait
#beta: females preference strength
#cost: cost of the sexual trait in males
#e.var: Defines different modes of environmental variation: Step, Random, Directional and None
#directional.rate: Strength of environmental change when it is directional - mean change per timestep
#random.sd1: Standard deviation of "ordinary" change when e.var is random
#random.sd2: Standard deviation of "rare event" change when e.var is random
#random.p.rare: Probability per timestep of a rare event when e.var is random
#GxE: Genotypes per environment, can be True or False
#harvest_intensity: proportion of the population harvested each time unit
#harvest_type: what sort of hunting? options are "random" - individuals taken at random regardless of sex or condition, or "selective" - males with the largest ornaments are harvested preferentially
#harvest_selection - how selective is the harvest? 2=very, 1=quite, 0.1=not much, 0=random

#harvest_threshold_prop: a threshold population size below which there is no harvest. Calculated as a proportion of K. Set to 0 to give a constant exploitation rate management.

```
simulation_SS<-function(b=0.5, d=0.08, K=200, N0=100, t=600, e= rnorm(1,mean=1,
sd=0.5), O=5, l=2, fem.sel=5, alpha=4, beta=10, cost=5, e.var="Random",
directional.rate=0.005, random.sd1=0.05, random.sd2=0.2, random.p.rare=0.01,
GxE=FALSE, harvest_intensity=0, harvest_type="random",
harvest_selection=1,harvest_threshold_prop=0){
```

Make sure all arguments are reasonable numbers

```
if(fem.sel<1| round(fem.sel)!=fem.sel){
  stop("fem.sel must be an integer equal or bigger than 1")
}
```

```
if(O<1| round(O)!=O){
  stop("O must be an integer equal or bigger than 1")
}
```

```
if(l<1| round(l)!=l){
  stop("l must be an integer equal or bigger than 1")
}
```

```
if(alpha<0|beta<0|cost<0){
  stop("alpha, beta and cost must be equal or bigger than 0")
}
```

```
# Initial population
```

```
ind <- vector(mode="list", N0)#Empty list with N0 elements.
for(i in seq(ind)){
  ind[[i]]$alive <- 1 #1= alive, 0=dead
  ind[[i]]$sex <- sample(c("F","M"),1) #F= female, M= male
  ind[[i]]$genotype <- rnorm(1,mean=e, sd=0.75)
  ind[[i]]$sex.gen <- ifelse(fem.sel==1, runif(1, min=0, max=0.1), runif(1, min=1,
max=1.7))
  ind[[i]]$ind.e<- rnorm(1,mean=e, sd=0.2)#The environment for each individual
(microenvironments)
  ind[[i]]$mismatch <- (ind[[i]]$genotype-ind[[i]]$ind.e)^2
  if(ind[[i]]$sex=="M"){#Cost of the sexual attribute only for males, the higher the
absolute difference of the genotype with the environment (mismatch), the lower the
resources available for the attribute.
    ind[[i]]$sex.trait <- ind[[i]]$sex.gen/(1+(ind[[i]]$mismatch*alpha))
  }else{#close if, open else
    ind[[i]]$sex.trait <- (ind[[i]]$sex.gen*beta)/(1+beta)
  }#close else
  ind[[i]]$phenotype <- round(ind [[i]]$genotype)
  ind[[i]]$age <- round(runif(1, min=1, max=10))
}

is.male <- which(sapply(ind, function(x) x $sex) == "M" & sapply(ind, function(x) x$age)
> l) #list of males
is.female <- which(sapply(ind, function(x) x $sex) == "F" & sapply(ind, function(x)
x$age) > l)#list of females
```

```
#Vectors for recording pop. statistics:
```

```
lifespan<-NaN*(t/2)
```

```
mismatch.area<-NaN*(t/2)
```

```
strait<-NaN*(t/2)
```

```
e0<-e
```

```
round<-0
```

```
eff_pop<-0
```

```
# Calculate harvest threshold
```

```
harvest_threshold <- harvest_threshold_prop * K
```

```
#####SIMULATION#####
```

```
for(i in seq(t)){ # Loop for each time increment
```

```
  #ENVIRONMENTAL RESPONSE: The supply and lapply functions change all the  
  elements of the "ind" list at the same time:
```

```
  ind<-lapply(ind,function(x){x$age<- x$age+1; x})#Ageing
```

```
  is.male <- which(sapply(ind, function(x) x $sex) == "M" & sapply(ind, function(x)  
  x$age) > I) #list of males
```

```
is.female <- which(sapply(ind, function(x) x $sex) == "F" & sapply(ind, function(x)
x$age) > I)#list of females
```

```
is.not.male<- which(sapply(ind, function(x) x $sex) == "F" | sapply(ind, function(x)
x$age) <= I & sapply(ind, function(x) x$sex)=="M")#list of "no males": Females and
immature individuals
```

```
ind<-lapply(ind,function(x){x$ind.e <- rnorm(1,mean=e, sd=0.2); x})#Change in
"individual environment"
```

```
ind<-lapply(ind,function(x){x$mismatch <- (x$genotype-x$ind.e)^2; x})#Change in
mismatch
```

```
if(GxE!=TRUE){
  ind[is.male]<-lapply(ind[is.male],function(x){x$sex.trait <-
x$sex.gen/(1+(x$mismatch*alpha)); x})#Definition of display in males
  ind[is.female]<-lapply(ind[is.female],function(x){x$sex.trait <-
(x$sex.gen*beta)/(1+beta); x})#Definition of preference in females
}
```

```
#DEATH:
```

```
pop.e<-length(ind)/K #Population effect on death
```

```
#Death probability in males, including population effect, selection effect, sex trait
effect and age effect.
```

```
ind[is.male]<-lapply(ind[is.male],function(x){x$alive <-
ifelse(runif(1)<=d*(pop.e+x$mismatch+(abs(x$sex.trait)*cost)+(0.0154*(x$age)^2-
(0.169*x$age) + 0.46)),0,1); x})
```

```
#Death probability in females and immature individuals. Includes the same effects as
in males except the sex trait.
```

```

ind[is.not.male]<-lapply(ind[is.not.male],function(x){x$alive <-
ifelse(runif(1)<=d*(pop.e+x$mismatch+(0.0154*(x$age)^2- (0.169*x$age) + 0.46)),0,1);
x})
is.dead <- which(sapply(ind, function(x) x $alive) == 0)
if(length(is.dead) > 0){
  ind <- ind[-is.dead]

}#closes if

```

```

##### Harvesting #####

```

```

#### Random harvesting

```

```

population_size<-length(ind)

```

```

if(harvest_intensity>0) {

```

```

  if (harvest_type=="random" & population_size > harvest_threshold) {
    male.pop <- length(which(sapply(ind, function(x) x $sex) == "M" & sapply(ind,
function(x) x$age) > I)) #number of mature males

```

```

    is.alive <- which(sapply(ind, function(x) x$alive) == 1 & sapply(ind, function(x) x$age)
> I) #list of individuals who are alive and mature

```

```

    number_removed<-round(male.pop * harvest_intensity,0) #calculate number to be
harvested. Base this on the number of males because sex ratios are not necessarily

```

50:50. This means that random harvesting with harvest intensity set to x is removing the same number of individuals as selective harvesting with intensity set to x

```
rm(male.pop) #clean up
```

```
if(population_size - number_removed < harvest_threshold) number_removed <-  
population_size - harvest_threshold #Don't let harvesting take the population below the  
threshold
```

```
removed<-sample(is.alive, size=number_removed, replace=FALSE) #random  
selection of individuals to be harvested
```

```
if(length(removed)>0) ind <- ind[-removed] #Removal of harvested individuals
```

```
}
```

```
#### Selective harvesting of males only
```

```
if(harvest_type=="selective" & population_size > harvest_threshold) {
```

```
is.male <- which(sapply(ind, function(x) x $sex) == "M" & sapply(ind, function(x)  
x$age) > I) #list of males
```

```
temp1<-sapply(ind, function(x) x$sex.trait)
```

```
male_sex_traits <- cbind(temp1[is.male], is.male) #Extract values for sex.trait for  
males, put it in a matrix with the index values for each individual
```

```
rm(temp1)
```

```
colnames(male_sex_traits)<-c("sex_trait","index")
```

```
male_sex_traits<-data.frame(male_sex_traits)
```

```
male_sex_traits<-dplyr::arrange(male_sex_traits,desc(sex_trait)) #Order  
male_sex_traits by the value of sex_trait in descending order
```

```
number_removed<-round(length(is.male) * harvest_intensity,0) #calculate number to  
be harvested
```

```
if(population_size - number_removed < harvest_threshold) number_removed <-  
population_size - harvest_threshold #Don't let harvesting take the population below the  
threshold
```

```
weights<-1/((1:length(is.male))^harvest_selection) #Calculate weighting on the basis  
of rank order of sex.trait
```

```
weights<-weights/sum(weights) #Make the weights sum to 1
```

```
if(number_removed>0) {
```



```
removed<-sample(male_sex_traits$index, size=number_removed, replace=FALSE,  
prob=weights) #Get index values for the males with the largest sex traits to be  
removed
```

```
ind <- ind[-removed] #Removal of harvested individuals  
}  
}  
  
}
```

```
#Break the main loop if all individuals are dead (length(ind)==0).
```

```
extinct<-ifelse(length(ind)==0, 1,0)
```

```
extinction.t<-ifelse(extinct==1,i,NA)
```

```
if(extinct==1) break
```

```
is.male <- which(sapply(ind, function(x) x $sex) == "M" & sapply(ind, function(x) x  
$age) > I) #list of males
```

```
is.female <- which(sapply(ind, function(x) x $sex) == "F" & sapply(ind, function(x) x  
$age) > I)#list of females
```

```
##MATE CHOICE: The list "reproduction" specifies which female mates with which  
male.
```

```
#The list gives also the number of newborns per female.
```

fem.sel2<-ifelse(fem.sel>length(is.male),length(is.male),fem.sel)#Modifies the list of males if the number of available males is shorter than the amount of males from which each female chooses a mate.

male.att<-median(sapply(ind[is.male], function(x) x\$sex.trait))

reproduction<-vector(mode="list", length(is.female))

#This "if" prevents errors that arise when there are no mature males left during a time step (length(is.male)==0)

if (length(is.male)>0){

 loop.nb<-1

 j<-3

 for(j in is.female){

 reproduction[[loop.nb]]\$female <- j#Identity of the female

 reproduction[[loop.nb]]\$offspring <- O-round(ind[[j]]\$mismatch)#Amount of offspring per female depending on mismatch

 reproduction[[loop.nb]]\$offspring <- ifelse(reproduction[[loop.nb]]\$offspring<0,0,reproduction[[loop.nb]]\$offspring)#Offspring can't be negative

 reproduction[[loop.nb]]\$preference <- ind[[j]]\$sex.trait#preference of the female

 reproduction[[loop.nb]]\$list.males <- sample(is.male,fem.sel2)#List of males from which the female will select the mate

#attractiveness for each male. Includes a random factor which depends on the median of the sexual display in males (rnorm(1,mean=0, sd=male.att/10))

```
reproduction[[loop.nb]]$att <- sapply(ind[reproduction[[loop.nb]]$list.males],
function(x) x$sex.trait)*reproduction[[loop.nb]]$preference#+rnorm(1,mean=0,
sd=abs(male.att)/2)
```

```
reproduction[[loop.nb]]$att <- sapply(reproduction[[loop.nb]]$att, function(x)
x+(rnorm(1,mean=0, sd=abs(male.att)/10)))
```

```
reproduction[[loop.nb]]$themale<-
reproduction[[loop.nb]]$list.males[which(max(reproduction[[loop.nb]]$att)==reproduction
[[loop.nb]]$att)]#Selection of the most attractive male
```

```
reproduction[[loop.nb]]$themale<-ifelse(length(reproduction[[loop.nb]]$themale)>1,
sample(reproduction[[loop.nb]]$themale, 1),reproduction[[loop.nb]]$themale)#Selection
of only one male if there are many males with the same attractiveness
```

```
loop.nb<-loop.nb+1
```

```
} # Close loop
```

REPRODUCTION How many new individuals will be born from each female. Each birth event has its own independent birth probability. This is done with the function replicate().

#In order to avoid errors, the amount of newborns is directly set to 0 without the replicate() function when the female's offspring is=0

```
reproduction<-lapply(reproduction,function(x){x$newborns
<-ifelse(x$offspring==0,0,sum(replicate(x$offspring, ifelse(runif(1)<=b*(1 -
length(ind)/K),1,0)))) ; x})
```

#The reproduction list is simplified in a data frame (new.features). This data frame gives the identity of the male and the female mating and the amount of new individuals

#that they are adding to the population. The new.features data frame will be used to define the features of the new individuals.

```
newborns<-sapply(reproduction, function(x) x$newborns)
```

```
female<-sapply(reproduction, function(x) x$female)
```

```
male<-sapply(reproduction, function(x) x$themale)
```

```
new.features<-matrix(nrow=length(is.female), ncol=3, c(newborns,male,female))
```

```
reproductives<-0
```

#This "if" prevents errors that arise when there are no new individuals born in a time step

```
if(sum(newborns>0)){
```

```
  new.features<-subset(new.features, newborns>0)
```

```
  new.features2<-matrix(nrow=sum(new.features[,1]), ncol=3)
```

#This loop multiplies the row of every couple in new.features according to the amount of new individuals that they are producing.

#e.g. if a couple (male+female) will give two newborns, its row is duplicated in the new.features data frame. This will

```
#allow to define the features of the new individuals
for (n in (seq(nrow(new.features)))){
  new.features2<-rbind(new.features2,
t(replicate(new.features[n,1],new.features[n,])))
}
```

```
colnames(new.features2)<-c("Newborns", "Males", "Females")
```

```
new.features<-data.frame(new.features2)
new.features<-new.features[complete.cases(new.features),] #Remove the NA
generated
```

```
#The new individuals are stored in a new list (new.ind):
new.ind <- vector(mode="list", nrow(new.features))#Number of elements=number
of newborns in each time step
```

```
#The features of each individual are defined with lapply() if possible to avoid loops
new.ind<-lapply(new.ind,function(x){x$alive <-1; x})#Alive
new.ind<-lapply(new.ind,function(x){x$sex <-sample(c("F","M"),1); x})#Sex
```

```
new.male <- which(sapply(new.ind, function(x) x $sex) == "M")#New males
new.female <- which(sapply(new.ind, function(x) x $sex) == "F")#New females
```

```
#Vectors with the genotype and sexual genotype of the reproductive couples.
Since the rows in the new.features data frame
#are repeated according to the number of newborns for each couple, the parental
features will be repeated according to the number of new
```

```
#individuals that will inherit these features.  
fem.gen<-sapply(ind[new.features$Females], function(y) y$genotype)  
male.gen<-sapply(ind[new.features$Males], function(y) y$genotype)  
fem.sgen<-sapply(ind[new.features$Females], function(y) y$sex.gen)  
male.sgen<-sapply(ind[new.features$Males], function(y) y$sex.gen)
```

```
#This loop defines the sexual and condition genotype of each new individual  
depending of the genetic features
```

```
#of the parents. Since there are the same number of rows in new.features than  
elements in the new.ind list, the repeated genetic
```

```
#features of the parents coincide with those of every new individual (e.g.  
new.ind[[1]] has the genetic features of fem.gen[1] and male.gen[1])
```

```
for(m in seq(new.ind)){
```

```
#The genotypes of each new individual are calculated as the mean of the  
genotypes of the parents + a random number
```

```
# pulled out of a normal distribution (mean=0, sd =0.05)
```

```
new.ind[[m]]$genotype<-mean(c(fem.gen[m], male.gen[m]))
```

```
new.ind[[m]]$genotype<-new.ind[[m]]$genotype+rnorm(1,mean=0, sd=0.05)
```

```
new.ind[[m]]$sex.gen<-mean(c(fem.sgen[m], male.sgen[m]))
```

```
new.ind[[m]]$sex.gen<-new.ind[[m]]$sex.gen+rnorm(1,mean=0, sd=0.05)
```

```
} # Close loop
```

```
#Definition of the other features in new.ind. Outside the loop, only using lapply.
```

```
new.ind<-lapply(new.ind,function(x){x$ind.e <-rnorm(1,mean=e, sd=0.2);  
x})#Individual environment
```

```
new.ind<-lapply(new.ind,function(x){x$mismatch <-(x$genotype-x$ind.e)^2;  
x})#Mismatch
```

```
new.ind[new.male]<-lapply(new.ind[new.male],function(x){x$sex.trait <-  
x$sex.gen/(1+(x$mismatch*alpha)); x})#Sexual display in males
```

```
new.ind[new.female]<-lapply(new.ind[new.female],function(x){x$sex.trait <-  
(x$sex.gen*beta)/(1+beta); x})#Preference in females
```

```
new.ind<-lapply(new.ind,function(x){x$phenotype <-round(x$genotype);  
x})#Phenotype
```

```
new.ind<-lapply(new.ind,function(x){x$age <-0; x})#Age=0
```

#Append new individuals to the ind list. They have the exact same structure, so only a simple append() function is needed

```
ind<-append(ind,new.ind)
```

```
}#close no newborns if
```

```
}#Close no-males if
```

```
#ENVIRONMENTAL VARIABILITY:
```

```
if (e.var=="Directional"){  
e<-ifelse(i<(t/4), e0+sample(c(-1,1),1)*runif(1, min=0,  
max=0.02),e<-e+rnorm(1,mean=directional.rate, sd=0.005) )
```

NB the "step" and "none" options were implemented in an earlier paper but not used here. They are retained for completeness.

```
}
```

```

if (e.var=="Step") {
  e0<-ifelse(i==round(t/4), e+1.25, e0)
  e<-e0+sample(c(-1,1),1)*runif(1, min=0, max=0.02)
}

if (e.var=="None") {
  e<-e0+sample(c(-1,1),1)*runif(1, min=0, max=0.02)
}

if (e.var=="Random") {
  e<-e+sample(c(rnorm(1,mean=0, sd=random.sd1),rnorm(1,mean=0,
sd=random.sd2)),1,prob=c(1-random.p.rare,random.p.rare))
}
if(e.var!="Random"& e.var!="None"& e.var!="Step"& e.var!="Directional"){
  stop("e.var must be either Directional, Step, Random or None")
}

#POPULATION STATS

if (i>=round(t/4) & i>round(3/4)){
  round<-round+1
  lifespan[round]<-mean(sapply(ind, function(x) x$age))
  mismatch.area[round]<-mean(sqrt(sapply(ind, function(x) x$mismatch)))
  strait[round]<-mean(sapply(ind, function(x) x$sex.trait),na.rm=T)
  # if(length(is.mature)>0){
    #Effective population size (Ne) calculated according to Wright's formulae:

$$4N_mN_f/(N_m+N_f)$$

    #
    eff_pop[round]<-(4*length(is.female)*length(is.male))/(length(is.female)+length(is.male))
  }
}

```



```
    # }  
  }  
  
}#close main loop  
  
# Statistics from run  
  
total.mismatch<-sum(mismatch.area, na.rm=T)  
median.lifespan<-median(lifespan, na.rm=T)  
median.strait<-median(strait, na.rm=T)  
# Ne<-mean(eff_pop, na.rm=T)  
factors<-paste(K,alpha,fem.sel,e.var,GxE, sep="")  
output<-c(total.mismatch, median.lifespan, median.strait, extinct, extinction.t,factors)  
return(output)  
  
}#Close function
```