MatSim: Monte Carlo simulation for the generation of mating tables

A. Carvajal-Rodríguez

Departamento de Bioquímica, Genética e Inmunología. Universidad de Vigo, 36310 Vigo, Spain.

*: A. Carvajal-Rodríguez. Departamento de Bioquímica, Genética e Inmunología. Universidad de Vigo, 36310 Vigo, Spain. Phone: +34 986813828

email: acraaj@uvigo.es

Abstract

In species with sexual reproduction, the mating pattern is a meaningful element for understanding evolutionary and speciation processes. Given a mating pool where individuals can encounter each other randomly, the individual mating preferences would define the matings frequencies in the population.

However, in every mating process, we can distinguish two different steps. First, the process of pair formation which implies that an encounter between partners must occur. Second, the actual mating once the encounter has occurred.

Yet, we cannot always assume that the observed population patterns accurately reflect the individual's preferences. In some scenarios the individuals may have difficulties to achieve their mating preferences, such as in monogamous species with low population size, where the mating process is similar to a sampling without replacement. In the latter, the encounter process will introduce some noise that may disconnect the expected individual preferences from the obtained mating pattern.

Actually, the difference between the mating pattern observed in a population and the mating preferences of the individuals have been shown by different modeling scenarios.

Here I present a program that simulates the mating process for both discrete and continuous traits, under different encounter models and individual preferences, including effects as drift, time dependence and aging. The utility of the software is demonstrated by replicating and extending, a recent study that showed how patterns of positive assortative mating, or marriage in human societies, may arise from non-assortative individual preferences. The previous result is confirmed and it is caused by the marriage among the "ugliest" and oldest individuals, who after many attempts were

finally able to mate among themselves. In fact, by introducing an aging process, I show how the assortative pattern vanishes provided that there is not assortative individual preference.

The software MateSim is available jointly with the user's manual, at

http://acraaj.webs.uvigo.es/MatSim/MatSim.zip

Keywords: preference functions, mating tables, mate choice, assortative, encounter-mating, correlation.

1. Introduction

In every mating process we can distinguish two key steps. First, the process of pair formation which implies that an encounter between partners must occur. Second, once the encounter happens, the mutual individual preferences take action by accepting or rejecting the mate.

Yet, we should distinguish between individual mating preferences and the observed population mating patterns. The latter is what we care about from an evolutionary perspective. Obviously, in some scenarios, as polygamous or monogamous species with high population sizes, the individuals have a better opportunity to attain their mating preferences than in other scenarios such as monogamous species with low population size, in which the mating process is similar to a sampling without replacement (from the point of view of available partners). In the former, the population pattern would resemble the individual preferences more precisely while in the latter, the encounter process will introduce some noise that disconnect the expected individual mating preferences from the obtained mating pattern (Gimelfarb, 1988a, b).

Moreover, the difference between the mating pattern observed in a population and the mating preferences of the individuals, have been evidenced by modeling scenarios that produce positive assortative mating without assortative individual preferences (Burley, 1983; Xie et al., 2015).

In general, it seems not to make much sense to assume the existence of preferences within a mating scheme that produces random-like patterns or vice versa, no individual preferences that systematically generate specific population patterns. One may ask, how did such preferences evolve? Alternatively, a population pattern that is not sustained by genetically determined preferences would have no evolutionary outcome.

Therefore, although occasionally the individual preference and the population pattern may be disconnected, this may not be the usual scenario.

Most models assume that the encounter is random, although depending on the species this random encounter can be serial i.e. individual by individual, or in groups, leks, etc. In addition, the species may be polygamous (models with replacement) or monogamous, the latter implying that when a pair is formed these individuals are taken out from the mating pool.

A monogamous species may still resemble a mating model with replacement if the population size is high enough to permit that the mating sample is only a fraction of the whole population, so that the frequencies of available phenotypes are not altered during the mating process. However, if the population size is low, the process of mating in a monogamous species will resemble a model without replacement.

In any case, once the encounter happens, the mating depends on the individual preferences between partners. Therefore, it is interesting to explore how different encounter models interact with the individual preferences, in order to get a better understanding on how the population mating pattern and the individual mating preference are connected (Burley, 1983).

Simulation is a key tool for exploring mate choice evolution scenarios (Carvajal-Rodriguez and Rolán-Alvarez, 2014; Fernández-Meirama et al., 2017; Rolan-Alvarez et al., 2015; Xie et al., 2015). In the present work, I propose a mating simulation software that allows the generation of mating tables under different kinds of traits, encounters and preferences. The program may be useful for exploring the relationship between mating preferences and the observed population pattern under different conditions. It

may also be useful for testing different non-random mating and sexual selection estimators.

I demonstrate the software by replicating a recent study that utilized a continuous encounter mating (EM) model to show how patterns of positive assortative mating may arise from non-assortative individual preferences (Xie et al., 2015).

2. Software description

2.1 General algorithm

MatSim performs Monte Carlo simulation of mating tables under different discrete or continuous trait models. The general algorithm is quite simple (Fig. 1).

1. Generate a population of size N with trait values obtained from a normal (continuous traits) or uniform (discrete traits) distribution
2. Get $n_1 = N / (1 + \text{OSR})$ females and $n_2 = N - n_1$ males
3. Form a random pair of male and female
4. Check sterility associated with aging (only in continuous models with aging)
5. Get the pair mating probability (depending on the continuous or discrete preference model)
6. Fertile partners decide mating based on their mating probability
7. If necessary (no replacement) update the frequencies in the individual pool
8. Return to step 3 until the desired sample is obtained or the available individuals are exhausted
9. Write the output as a mating table (discrete traits) or mating pairs (continuous trait)

Fig 1. Algorithm for simulating mating pairs. OSR: operative sex ratio.

The first step consists in generating a population of individuals either from a normal distribution if the mating trait is continuous, or different phenotypic classes from a uniform distribution, if we require different class counts for a given discrete trait.

Next, individuals are separated in two sexes as given by the operational sex ratio, which is the ratio of sexually competing males and females that are ready to mate (Clutton-Brock, 2007).

The following step is a key point in the algorithm and refers to the way in which the random encounter occurs between individuals.

2.2 Pair formation process

This corresponds to the step 3 in the mating algorithm (Fig. 1). I distinguish two main processes of pair formation: with or without replacement of mating types.

When the availability of individuals is not affected by matings that have already occurred, the expected mating pattern in the population is completely determined by the population frequencies and the individual preferences. Thus, the process of pair formation can be viewed as sampling with replacement (SR models) from the set of population types. Polygamous species or monogamous in which only a fraction of the population mate during a given mating season, are adequately described by this type of pair formation.

On the contrary, when matings are monogamous and most of the population do actually mate, the proportion of available individuals for mating must be updated after each encounter event (sampling without replacement from the pool of population types).

Processes of the latter kind are the so called encounter-mating (EM) models (Gimelfarb, 1988b).

MatSim simulates mating data under both type of processes of pair formation, with replacement (SR models) or without replacement (EM models), from the population phenotypes. The SR models do not require any update of the individual pool during the mating process. On the contrary, the EM models require that the individual pool is updated after each mating round. In the case of the EM models I distinguish individual EM, in which only an encounter takes place at a time, and mass EM, in which more than one pair can be formed simultaneously (Gimelfarb, 1988b).

See Tables S1 and S2 in the manual of the program for a detailed explanation on how to define the different pair formation models.

2.3 Aging in continuous models

When the preference model is for continuous traits, i.e. the matings are not tabulated by phenotypic classes, we take into consideration each given individual in the population. In this case, after the pair formation we may evaluate the aging state of the pair. This corresponds to the step 4 in Fig. 1. The aging is optional, if the model was defined without aging this step is omitted.

However, it seems realistic to consider that, independently of the mating trait, the mating probability of an individual decreases with age. The latter may occur because the individual becomes old or sterile or simply he/she has not enough energy to invest in mating.

Without loss of generality, when an individual enters the absorbing state of not being able of mating because of aging, we say that the individual is sterile. I model the aging process regarding to mating, by means of the Weibull distribution. This distribution is versatile and is adequate for modeling survival and time-to-failure processes. In our context, the survival function $R(t)$ represents the probability that at age t an individual is not yet sterile.

$$R(t) = Prob(T > t) = exp[-\left(\frac{t-\gamma}{\alpha}\right)^{\beta}] \qquad \text{if } t - \gamma \geq 0 \text{ or 1 otherwise.}$$

The random variable T represents the age to sterility, γ is the age from which an individual may be sterile; α represents the 63-percentile i.e. the age (counted from age γ i.e. $\alpha = t - \gamma$) at which 63% of the population is sterile and β is the shape parameter that stands for the increasing risk of being sterile. Thus, if $\beta = 2$, the increase of sterility is linear with age while if $\beta > 2$ the risk of sterility increases faster at higher age.

The age is measured in terms of mating attempts until married (EM models) or until the mating season ends (sampling with replacement model). Thus, I define the age of an individual as the natural logarithm of the mating attempts. Note that each mating attempt requires a new random encounter between any two available individuals of different sex. Therefore, under the EM models, once a pair is established, the age of both partners stop increasing.

After encounter, the aging state of female i and male j is evaluated. If the individual's age is above γ then the sterility state is checked previous the computation of the mating probability. An individual is considered sterile at time t when $U \geq R(t)$ where U belongs to *uniform*(0,1). If the individual happened to be sterile it is discarded from the population.

2.4 Mating under discrete preference models

These models imply a discrete trait involved in the preference process. The models are defined by the preferences and their expected effect (Fig. 2). The saturated model has *K*-1 parameters where *K* is the product of the number of different female and male types. The saturated individual preference model would produce sexual selection plus assortative mating pattern provided that the individual preferences are reflected in the observed matings. Models with just one parameter may produce female or male sexual selection or positive or negative assortative mating (sexual isolation, Fig. 2). These preference models or any other desired by the user, can be defined into the program.

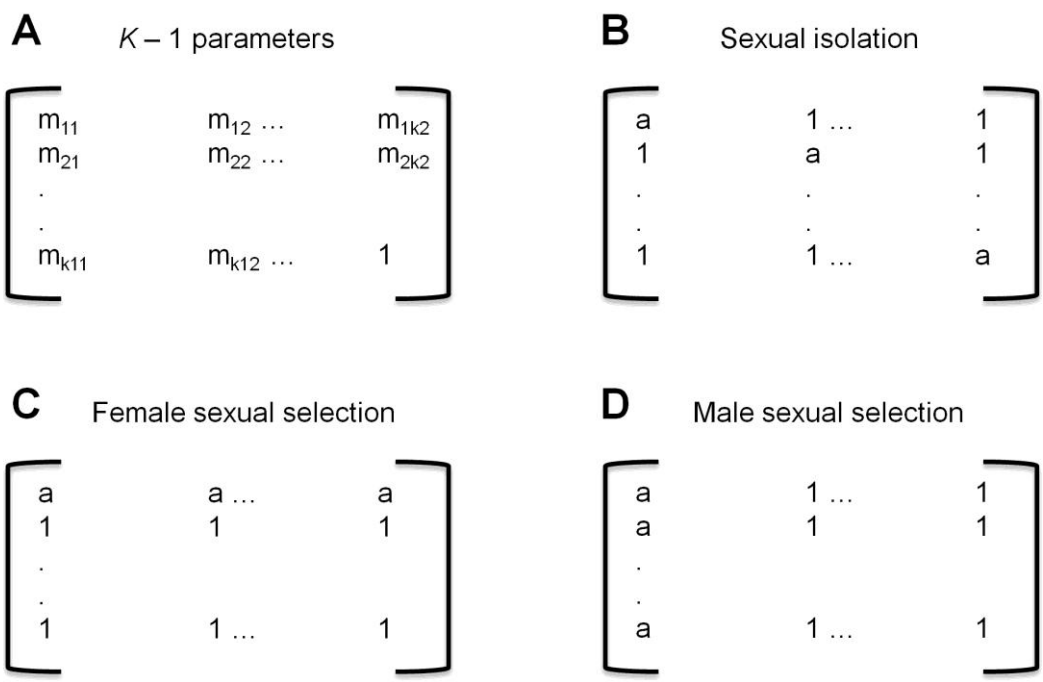

Fig 2. Discrete preference models defined by their expected effects. Females correspond to rows, males to columns.

The implementation of the mating also require the population phenotype frequencies, which can be uniform or user defined. Once the population frequencies and the mating propensities are defined, the expected number of occurrences for each mating type $i \times j$ is (Carvajal-Rodriguez, 2016)

$$Q(\mathrm{i,j}) = n \times p_{1\mathrm{i}} \times p_{2\mathrm{j}} \times m_{\mathrm{ij}} \ / \ M \qquad (1)$$

where $p_{1\mathrm{i}}$ and $p_{2\mathrm{j}}$ are the i female and j male population frequencies respectively, n is the sample size and $M = \sum p_{1\mathrm{i}} \times p_{2\mathrm{j}} \times m_{\mathrm{ij}}$.

The m_{ij} values correspond to the individual preferences and will depend on the desired model. Note that under EM type models, the phenotype frequencies are updated accordingly after each mating round.

The expectation in (1) should be accomplished for the SR models, or even for the EM ones when the mating sample size is lower than the given population size. However, when the sample size is close to the population size, the obtained mating pattern can be quite different from the expected.

The format of the obtained mating tables is the same as the JMating (Carvajal-Rodriguez and Rolan-Alvarez, 2006) and InfoMating (Carvajal-Rodriguez, 2017) input files (see the program manual).

2.5 Mating under continuous preference models

I implement a general preference function for the continuous model as

$$f = exp\ (\alpha_0 + \alpha_1 Z) \qquad (2)$$

2.5.1 Gaussian models

The Gaussian similarity models (Carvajal-Rodriguez and Rolán-Alvarez, 2014) are obtained by taking $\alpha_0 = 0$, $\alpha_1 = -f(C/s)$ and $Z = (D_{ij} - b)^2$, where b is the bias (see below) and D_{ij} is the absolute value of the difference between the female i and male j phenotypes for the similarity trait.

The function f is a quotient between the choice C and the tolerance s, that varies depending if the function is FND (Carvajal-Rodriguez and Rolán-Alvarez, 2014) or BD03 (Bolnick and Doebeli, 2003); the value of b is in $[0, D_{max}/2)$ for associative positive, or fixed to D_{max} for associative negative (see Appendix A for details).

Given an encounter and the preference function value f_{ij}, the mating probability for a pair i,j will be

$$p_{ij} = f_{ij} / f_{max}$$

where f_{max} is the maximum preference over the available matings.

2.5.2 Logistic models

Logistic preference models (Xie et al., 2015) may be obtained from (2) by considering the probability for any female F to mate with male j (i.e. the probability of male j to be accepted)

$$p^F_j = f_j / (1+f_j) = 1 / (1+ f_j^{-1})$$

with

$$f_j = exp(\beta_0 + \beta_1 Z_j^m) = exp(X_j^m)$$

and Z^m_j is the trait value of male *j*.

The male trait value Z^m_j transforms into the binary output of acceptance of marriage from the point of view of any given female, by means of the logistic variable $X^m_j = \beta_0 + \beta_1 Z^m_j$.

Similarly, the probability for any male *m* to mate with female *i* (the probability of female *i* to be accepted) implies

$$p^m_i = f_i / (1+f_i) = 1 / (1+ f_i^{-1}).$$

with

$$f_i = exp(X_i^f)$$

and $X^f_i = \alpha_0 + \alpha_1 Z^f_i$.

The current implementation of MatSim considers only equal female and male parameters so that $\alpha_0 = \beta_0$ and $\alpha_1 = \beta_1$.

The mating probability after encounter for a pair *i,j* will be

$$p_{ij} = p^f_j \times p^m_i.$$

2.5.3 Decreasing in time choosiness (impatience for mating)

As considered, both under Gaussian and logistic models, the choosiness characteristic of the individuals is constant through time. However, we could consider an scenario where single individuals become impatient as time passes and an increasing number of

marriages are performed, especially if neither polygamy nor divorce is allowed (Xie et al., 2015). Therefore, as time progressed the individuals become less choosy proportional to the number of marriages already performed (see details of the implementation in the appendix A).

3. Applications

Following, I demonstrate the use of the simulator for continuous preference models. The use of discrete models is left for an upcoming work.

I replicate a recent study that utilized a continuous EM model to show how patterns of positive assortative mating, or marriage in human societies, may arise from non-assortative individual preferences (Xie et al., 2015).

I confirm the previous result and demonstrate that the positive correlation is provoked by the marriage among the "ugliest" and oldest individuals, who after many attempts were finally able to mate among themselves. In fact, by introducing an aging process, the assortative pattern vanishes.

I use the same parameter values as in the original study. The population consists in n_1 = 5,000 females and n_2 = 5,000 males and the logistic parameters $\alpha_0 = -1$ and $\alpha_1 = 2$. When appropriate, the factor for impatience is c = 0.0005 and finally, I extend the original model by setting the aging process $\alpha = 5$, $\beta = 2$ and $\gamma = 1$.

The only difference between this implementation and the original, is that I allow a maximum of $n_1 \times n_2$ = 25,000 mating attempts. This means that if the matings were uniformly distributed, we "only" allow that each individual may attempt to mate 5,000 times, which in average, gives a maximum of one attempt with every individual from

the other sex. Since the matings are not uniformly distributed because some individuals may spend only few tries, this means that some may try more than 5,000 attempts.

The results are shown in Table 1. Since in the original study all correlation measures gave a similar result, I have only utilized one of such measures, namely, the overall correlation over the mating pairs. The model i-EM corresponds to the encounter mating model while the impatient i-EM corresponds to the version with increased probability of mating as time increases. We observe an overall correlation of 0.55 ± 0.001 and 0.44 ± 0.001 that is similar to the obtained 0.53 and 0.44 for the same scenarios in the aforementioned study.

I have also considered an encounter mating model in which several pairs can be formed simultaneously (mass-EM), the result is similar (0.42) but the correlation clearly declines (0.16) when the mass model is extended to the impatient version.

TABLE 1. Effect of pair formation and aging under a logistic preference function. The population size is 10,000 with equal proportion of males and females. The mating effort refers to the % of the population that is required to mate. The mating success refers to the final number of successful matings.

Model	Mating effort	Mating success	Correlation	Mean population age (mating attempts)
SR	100%	5000	0.001 ± 0.001	8
i-EM	100%	4997	0.5458 ± 0.001	4839
impatient i-EM	100%	5000	0.4421 ± 0.001	52
mass-EM	100%	5000	0.4208 ± 0.001	209

impatient mass-EM	100%	5000	0.1553 ± 0.001	6
i-EM with aging	100%	2696	0.0548 ± 0.002	5
i-EM	90%	4500	0.3740 ± 0.001	129
i-EM	80%	4000	0.2502 ± 0.002	52
i-EM	60%	3000	0.0775 ± 0.002	20
i-EM	50%	2500	0.0377 ± 0.002	14

SR: sampling with replacement; i-EM: individual-encounter mating; mass-EM: mass-encounter mating.

As already commented, it seems more realistic to incorporate an aging component to the model. This is clearly justified in the present case where, when expressing the age in terms of mating rounds or attempts, we appreciate that the average age in the i-EM model is almost 5,000 attempts per individual (Table 1).

The parameters for the aging model were $\alpha = 5$ which means that after $e^5 \approx 148$ mating attempts, the 63% of the individuals are sterile, $\beta = 2$ i.e. a linear increase of sterility with age, and $\gamma = 1$ that implies that the possibility of sterility begins after 3 attempts.

When this aging model is incorporated to the i-EM model, the correlation disappears (0.05) corroborating that the assortativeness was caused by an increased homogeneity in the oldest unmarried pool (Xie et al., 2015). The average age, in terms of mating attempts, collapses to 5 which is far less than the 4,839 attempts in the model without aging.

Even if we use a delayed aging model in which the occurrence of sterility is only possible after 55 mating attempts ($\gamma = 4$) , the obtained correlation is 0.24 which is still far below the value observed without aging.

This seems to confirm the pattern, already observed under the model with mating impatience, indicating that the incorporation of more realistic effects, diminishes the observed assortativeness.

Finally, I compare other i-EM models in which not all the adult population is required to marry. A mating effort of 90% implies that 10% of the adult population remains unmarried. Thus, with 10-20% of unmated individuals the correlation fails to 0.37-0.25 respectively, and mostly vanishes when the unmated individuals are 40-50% (0.08-0.04).

4. Conclusions

MatSim is a flexible and versatile tool for simulating different mating processes. It distinguishes between the pair formation and the mating, and also manages continuous or discrete models. It may be useful for evolutionary studies of mate choice. As a demonstration of the program, I have reviewed a study about dynamic processes of marriage in closed systems, and show that after the addition of aging to the original model, the assortative mating pattern obtained without assortative preference, tend to dissapear.

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Bibliography

Bolnick, D.I., Doebeli, M., 2003. Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. Evolution 57, 2433-2449.

Burley, N., 1983. The meaning of assortative mating. Ethology and Sociobiology 4, 191.

Carvajal-Rodriguez, A., 2016. Non-random mating and information theory. bioRxiv.

Carvajal-Rodriguez, A., 2017. InfoMating, p. Model selection and multimodel inference from mating frequency data to study sexual selection and sexual isolation effects.

Carvajal-Rodriguez, A., Rolan-Alvarez, E., 2006. JMATING: a software for the analysis of sexual selection and sexual isolation effects from mating frequency data. BMC Evol Biol 6, 40.

Carvajal-Rodriguez, A., Rolán-Alvarez, E., 2014. A comparative study of Gaussian mating preference functions: a key element of sympatric speciation models. Biological Journal of the Linnean Society 113, 642-657.

Clutton-Brock, T., 2007. Sexual Selection in Males and Females. Science 318, 1882-1885.

Fernández-Meirama, M., Carvajal-Rodríguez, A., Rolán-Alvarez, E., 2017. Testing the role of mating preference in a case of incomplete ecological speciation with gene flow. Biological Journal of the Linnean Society 122, 549-557.

Gimelfarb, A., 1988a. Processes of pair formation leading to assortative mating in biological populations: Dynamic interaction model. Theoretical Population Biology 34, 1.

Gimelfarb, A., 1988b. Processes of Pair Formation Leading to Assortative Mating in Biological Populations: Encounter-Mating Model. The American Naturalist 131, 865-884.

Lipowski, A., Lipowska, D., 2012. Roulette-wheel selection via stochastic acceptance. Physica A: Statistical Mechanics and its Applications 391, 2193-2196.

Rolan-Alvarez, E., Carvajal-Rodriguez, A., de Coo, A., Cortes, B., Estevez, D., Ferreira, M., Gonzalez, R., Briscoe, A.D., 2015. The scale-of-choice effect and how estimates of assortative mating in the wild can be biased due to heterogeneous samples. Evolution 69, 1845-1857.

Xie, Y., Cheng, S., Zhou, X., 2015. Assortative mating without assortative preference. Proceedings of the National Academy of Sciences 112, 5974-5978.

Appendix A. Preference functions for continuous traits

A general preference function for continuous traits is

$$f = exp\ (\alpha_0 + \alpha_1 Z) \qquad \text{(A-1)}$$

Gaussian similarity model

The Gaussian similarity models (Carvajal-Rodriguez and Rolán-Alvarez, 2014) are obtained by taking $\alpha_0 = 0$, $\alpha_1 = -f(C/s)$ and $Z = (D_{ij} - b)^2$, where b is the bias (see below) and D_{ij} is the absolute value of the difference between the female i and male j phenotypes for the similarity trait.

In the case of FND (Carvajal-Rodriguez and Rolán-Alvarez, 2014), the value of the choice C and tolerance s, enters the function f as $f(C/s) = (C/(sD_{max}))^2$ and the bias b is in $[0, D_{max}/2)$ for associative positive or fixed to D_{max} for associative negative preference functions.

In the case of BD03 (Bolnick and Doebeli, 2003), the value of the choice C and tolerance s, enters the function f as $f(C/s) = 0.5(C^2/s)^2$ and the bias b is 0 for associative positive or fixed to D_{max} for associative negative preference functions.

Given an encounter and the preference function value f_{ij}, the mating probability for a pair i,j will be

$$p_{ij} = f_{ij} / f_{max} \qquad \text{(A-2)}$$

where f_{max} is the maximum over the available matings.

The above implementation follows a roulette-wheel selection by stochastic acceptance algorithm (Lipowski and Lipowska, 2012).

Logistic Model

Logistic models may be obtained from (A-2) by taking the probability for any female *F* to mate with male *j* (i.e. the probability of male *j* to be accepted) to be

$$p^F_j = f_j / (1+f_j) = 1 / (1+ f_j^{-1})$$

with

$$f_j = exp(\beta_0 + \beta_1 Z_j^m) = exp(X_j^m)$$

and Z^m_j is the trait value of male *j*. The male trait value Z^m_j transforms into the binary output of acceptance of marriage from the point of view of any given female, by means of the logistic variable $X^m_j = \beta_0 + \beta_1 Z^m_j$.

Similarly, the male mating probability with female *i* (the probability of female *i* to be accepted) implies

$$p^m_i = f_i / (1+f_i) = 1 / (1+ f_i^{-1}).$$

with

$$f_i = exp(X_i^F)$$

and $X^F_i = \alpha_0 + \alpha_1 Z^F_i$.

The mating probability after encounter for a pair *i,j* will be

$$p_{ij} = p^F_j \times p^m_i \qquad \text{(A-3)}$$

Decreasing in time choosiness (impatience for mating)

For the Gaussian preference the "impatience" is implemented as $f(C/ s_t)$ where $s_t = s \times (n_t + 1)$ is the tolerance multiplied by the number of existing marriages at time t plus one. In the current implementation $s_t = s$ by default, this can be changed by means of the tag *-impatience* which if different from 0 defines the impatient behavior (see the program manual).

The impatience for the logistic is (Xie et al., 2015)

$$X^f_i = \alpha_0 + c_i n_t + \alpha_1 Z^f_i$$

$$X^m_j = \beta_0 + c_j n_t + \beta_1 Z^m_j.$$

where c_i, c_j are constants and n_t stands for the number of existing marriages at time t.

In the current implementation $c_i = c_j = c = 0$ by default. The value of c can be changed, say to 0.001, by the tag

-impatience 0.001

Note that (provided that c is positive for the logistic case) as n_t increases the mating probabilities tend to 1 independently of the mating trait, so the mating becomes less selective.

Aging: Weibull model

The survival function $R(t)$ represents the probability that at age t an individual is not yet sterile.

$$R(t) = Prob(T > t) = exp[-\left(\frac{t-\gamma}{\alpha}\right)^{\beta}] \qquad \text{if } t - \gamma \geq 0 \text{ or 1 otherwise.}$$

The random variable T represents the time to sterility, γ is the age from which an individual may be sterile; α represents the 63-percentile i.e. the age (counted from age γ i.e. $\alpha = t - \gamma$) at which 63% of the population is sterile and β is the parameter for the increasing risk of being sterile. Then, if $\beta = 2$ the increase of sterility is linear with age while if $\beta > 2$ the risk of sterility increases faster at higher age.

The age is measured in terms of mating attempts until married (EM models) or until the whole mating season ends (sampling with replacement model). Because there can be many attempts we use a logarithmic scale so that the age of an individual is the natural logarithm of its number of mating attempts.

The implemented continuous preference model by default assumes no age structure, so that $R(t) = 1$ for every age. The aging settings can be defined by the tag

-age_params 5 2 1

that introduces the values $\alpha = 5$, $\beta = 2$ and $\gamma = 1$.

If we don't want the aging process we can simple put a negative sign to the gamma parameter so that

-age_params 5 2 -1

implies that there is not aging ($R(t) = 1$ for every age).

An individual is considered sterile at time t when $U \geq R(t)$ where U follows an *uniform*(0,1). If the individual happened to be sterile then it is discarded from the population. The iteration ends when the specified or available number of non-sterile individuals already mated.