

# Discrete-time simulator for multi-loci selection on a trait

CWEB technical report

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## Abstract

Simulates the time (number of generations) it takes a diploid population to reach a predefined optimum trait value. Selection acts on the (multi-locus) trait, and we compare the time to reach optimum for two reproduction schemes. This CWEB [1, 3, 2] technical report describes corresponding C code. CWEB documents may be compiled with `cweave` and `ctangle`.

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# 1 Copyright

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## 2 Introduction

We are interested in investigating if high fecundity and skewed distribution of offspring (HFSDO), in addition to selection acting on a multi-loci trait, drives rapid adaptation. In particular, does the combination of HFSDO and selection acting on a multi-loci trait enable more rapid adaptation than in the absence of HFSDO. Also, in the single-locus case, in both haploid and diploid case, we would like to know if HFSDO enables more rapid adaptation than a non-skewed reproduction mechanism.

The population size of our diploid population is constant at  $2N$ . In each generation, the  $2N$  diploid individuals randomly form  $N$  pairs. Each pair independently contributes offspring. We let  $X_i$  denote the random number of offspring of pair  $i$ , and the  $X_i$  are iid, and independent between generations. Let  $b, \alpha, \psi$  be positive constants; define  $\mathbb{1}(A) := 1$  if  $A$  holds, and zero otherwise; write  $[n]_0 := \{0, 1, \dots, n\}$  for  $n \in \mathbb{N} := \{1, 2, \dots\}$ ;  $[n] := \{1, 2, \dots, n\}$ . The law of  $X_i$  is said to be "skewed" if it is given by

$$\mathbb{P}(X_i = k) = \frac{b^\alpha}{(b+k)^\alpha} - \frac{b^\alpha \mathbb{1}(0 \leq k < \psi)}{(1+b+k)^\alpha}, \quad k \in [\psi]_0; \quad (1)$$

the parameter  $b$  shifts the distribution to allow for mass at zero. The distribution (1) is monotonically decreasing with increasing  $k$ . The law (1) is similar in form to the model by [5]. However, the model by [5] is a limit statement, and as such can only be used in theoretical calculations.

We compare the law (1) of  $X_i$  with a Poisson distribution with parameter  $\lambda > 0$ . For  $\alpha < 2$  the law (1) has a much heavier tail than the Poisson. The population size is constant at  $2N$  generations;  $N$  pairs of individuals independently contribute juveniles. The total number of juveniles generated in any given generation therefore needs to be at least  $2N$ . If the law of  $X_i$  is Poisson, we take  $\lambda \geq 2$ ; otherwise the sampling takes a long time since the total pool of juveniles is regenerated until the total count of juveniles is at least  $2N$ .

Given the allelic types  $g_{i,j}^{(1)}$  and  $g_{i,j}^{(2)}$  at locus  $j \in [L]$  of individual  $i \in [2N]$ , the trait

value of individual  $i$  is computed as

$$z_i = \frac{1}{L} \sum_{j \in [L]} \xi_j (g_{i,j}^{(1)} + g_{i,j}^{(2)}). \quad (2)$$

The trait value of the population is the average of the individual trait values.

The optimum trait value is denoted by  $z_0$ . Given the trait value  $z_i$  of individual  $i$ , the fitness is given by

$$w_i = \exp(-s(z_i - z_0)^2). \quad (3)$$

Equation (2) for the trait value allows one, for example, to consider linear effects of allelic types. By way of example, set  $\xi_j = 1$  for simplicity, and let homozygotes for type 0 be the fittest genotype, heterozygotes less fit, and homozygotes for type 1 the least fit. Then  $z_0 = 0$ , and if there's one locus, the possible fitness values are 1,  $e^{-s}$ , and  $e^{-2s}$ .

If, in any given generation, the number of juveniles ( $\sum_i x_i$ ) exceeds  $2N$ , we draw  $\sum_i x_i$  independent exponentials ( $T_i$ ), where  $T_i$  has rate  $w_i$ . The  $2N$  juveniles with the lowest times then form the next set of adults. The genotypes of the parents do not affect the number of juveniles contributed, rather indirectly the viability of the juveniles. The viability of a juvenile depends on its' genotypes.

### 3 Compile and run

Use `cweave` on the `.w` file to generate `.tex` file, and `ctangle` to generate a `.c` file. To compile an executable:

```
gcc <flags> discrete_linear.c -lm -lgsl -lgslcblas
```

The command to run simulations (assuming `a.out` is the executable) is

```
a.out <N> <L> <a> <b> <p> <s> <z> <e> <R> <r> <f>
```

where `N` is number of pairs, `L` is number of loci, `a` is parameter  $\alpha$ ; `b` is parameter  $b$ , the shift of the distribution; `p` is  $\psi$ , the offspring cutoff; `s` is the selection strength  $s$ ; `z` the optimum  $z_0$ ; `e` is the allowed distance  $\varepsilon$  from optimum; `R` is number of runs; `r` is a random seed, `f` is the name of the file storing the results, the time to reach optimum. If  $\alpha > 0$ , the law of  $X_i$  is assumed skewed; otherwise set  $\alpha = 0$  to sample from the Poisson with  $b$  taken as the parameter ( $\lambda$ ) for the Poisson.

By way of example,

```
a.out 50000 1 0. 2.1 10 10. 0. 0.000001 5 123 results.out
```

writes the following into `results.out`:

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## 4 Code

The configuration of the population is stored as a  $(2L) \times (2N)$  matrix, with rows denoting loci, and each column stores the types of one diploid individual. Rows 1 to  $L$  store the types an individual received from one parent, and rows  $L+1$  to  $2L$  store the types received from the other parent. Rows  $j$  and  $j+L$  for  $j \in [L]$  hold the types at locus  $j$ . The configuration of juveniles is stored in the same way.

The GSL library (see <https://www.gnu.org/software/gsl/>) is used for random number generation and sorting. If the number of juveniles exceeds  $2N$  in any given generation, the exponential times of the juveniles are sorted into ascending order, and the  $2N$  juveniles with the lowest times form the new set of adults. We set a maximum allowed number of juveniles for computer memory purposes.

## 4.1 Random number generator

A random number generator of choice is declared using the `GSL_RNG_TYPE` environment variable. The default generator is the ‘Mersenne Twister’ random number generator [4] as implemented in GSL.

5 `<random number generator 5> ≡`

declare the random number generator *rngtype*

```
gsl_rng * rngtype;
```

Define the function *setup\_rng* which initializes *rngtype*:

```
void setup_rng(unsigned long int seed)
```

```
{
```

set the type as *mt19937*

```
rngtype = gsl_rng_alloc(gsl_rng_mt19937);
```

```
gsl_rng_set(rngtype, seed);
```

```
gsl_rng_env_setup();
```

```
}
```

This code is used in chunk 13.



## 4.2 Definitions

We set the maximum number of juveniles for memory purposes.

6  $\langle$ object definitions 6 $\rangle \equiv$

```
#define MAX_JUVENILES 10000000
```

This code is used in chunk 13.

### 4.3 Draw values for $X_i$

Draw values for  $X_i$ ; the diploid juveniles. We have, for  $b, \alpha > 0$  some constants,

$$\mathbb{P}(X_i = k) = \frac{b^\alpha}{(b+k)^\alpha} - \frac{b^\alpha \mathbb{1}(0 \leq k < \psi)}{(1+b+k)^\alpha}, \quad k \in [\psi]_0,$$

and we observe that  $\sum_{0 \leq k \leq \psi} \mathbb{P}(X_i = k) = 1$ .

7  $\langle$  initialize distribution for  $X_i$   $\rangle \equiv$

```

void drawXi(int N, int psi, double a, double b, gsl_ran_discrete_t * Pmass, int
    *tXi, gsl_rng *r)
{
    /* N is number of pairs; psi is the truncation of the skewed offspring distribution
    (1); the number of juveniles contributed by each pair is stored in tXi; Pmass is
    the distribution (1) */
    int k, teljari;
    tXi[0] = 0;
    teljari = 0;
    /* we need the total number of juveniles to be at least 2N */
    while ((tXi[0] < 2 * N) & (teljari < 1000000)) {
        teljari = teljari + 1;
        tXi[0] = 0;
        for (k = 1; k <= N; k++) {
            /* if a > 0 we assume the skewed law (1); otherwise Poisson with parameter
            lambda = b */
            tXi[k] = (a > 0. ? (int) gsl_ran_discrete(r, Pmass) : gsl_ran_poisson(r, b));
            tXi[0] = tXi[0] + tXi[k];
        }
    }
}

```

```
        /* assert breaks the execution if the statement does not hold */  
        assert(teljari < 1000000);  
        assert(tXi[0] ≤ MAX_JUVENILES);  
    }
```

This code is used in chunk 13.

#### 4.4 Update population

Update population given values  $x_i$  of juveniles generated by each pair. The genotypes of the parents do not affect the number of juveniles contributed. Genotypes are assigned to each juvenile, and trait value computed. If the number of juveniles exceeds the population size  $2N$ , selection sorts out the  $2N$  fittest (on average) individuals. We randomly pair the parents; since we are not modeling fecundity selection, we can separately draw  $N$  numbers of juveniles, and then assign to randomly formed parent pairs.

The module *juvenile\_genotypes* returns the trait value of the  $2N$  juveniles that form the new set of adults.

8  $\langle$  assign juvenile genotypes 8  $\rangle \equiv$

```
double juvenile_genotypes(int N, int L, double s, double znull, double epsilon, int
    **Pop, int *indindex, int *tXi, gsl_matrix_int *tempJuve, double *Z, double
    *locuseffects, double *etimes, size_t *aindex, int *allelefr, gsl_rng *r)
```

```
{
```

```
/* N is number of pairs; L is number of loci; s is selection coefficient; znull is
optimum trait value; epsilon is maximum allowed distance from optimum; Pop is
the matrix for the population configuration of types; indindex is vector of indexes
for pairing the parents; tXi stores the N numbers of juveniles; Z stores the juvenile
trait values; tempJuve stores the type configuration of the juveniles; locuseffects
is the vector of the effects of loci, the  $\xi_j$  in (2); etimes stores the exponential times;
aindex storest the sorted indexes of juveniles; allelefr stores the count of an allele
of some type, for consistency check; r is the random number generator */
```

```
int i, j, k, B, xindex;
```

```
double Zbar = 0.;
```

```
allelefr[0] = 0;
```

```
/* tXi[0] =  $x_1 + \dots + x_N$  is the total number of juveniles */
```

```

xindex = 0;
for (i = 1; i ≤ N; i++) {
    /* check if pair i produced potential offspring, ie. if  $X_i > 0$  */

    if (tXi[i] > 0) {
        for (k = 1; k ≤ tXi[i]; k++) {
            for (j = 1; j ≤ 2 * L; j++) {
                /* if B takes value 0 we assign type from set [L], otherwise from set
                {L + 1, ..., 2L}; genotypes for range [L] are assigned from individual  $\sigma(i)$ ,
                otherwise from individual  $\sigma(N + i)$ , where  $\sigma$  denotes the permutation of
                the indexes */

                B = (int) gsl_ran_bernoulli(r, .5);

                gsl_matrix_int_set(tempJuve, j, xindex + 1, Pop[(j > L ? (B > 0 ? j :
                    j - L) : (B > 0 ? j + L : j))][(j > L ? indindex[N + i] : indindex[i])]);
            }

            /* now have assigned genotypes for juvenile, compute trait value */

            Z[xindex] = 0.;
            for (j = 1; j ≤ L; j++) {
                Z[xindex] = Z[xindex] + (locuseffects[j] *
                    ((double)(gsl_matrix_int_get(tempJuve, j,
                    xindex + 1) + gsl_matrix_int_get(tempJuve, j + L,
                    xindex + 1)))/((double) L));
            }

            /* given trait value z for juvenile, compute the fitness value
             $w = e^{-s(z-z_0)^2}$ , and draw exponential with rate w */

```

```

    etimes[xindex] = gsl_ran_exponential(r,
        1./gsl_sf_exp(-s * gsl_pow_2(Z[xindex] - znull)));
    xindex = xindex + 1;
}
}
}
assert(xindex == tXi[0]);

assert(tXi[0] >= N + N);
if (tXi[0] > 2 * N) {
    /* sort the times into ascending order, and store the sorted indexes in aindex */

    gsl_sort_index(aindex, etimes, 1, tXi[0]);

    /* the first 2N indexes in aindex are the indexes of the surviving juveniles */
    for (i = 0; i < N + N; i++) {
        Zbar = Zbar + Z[(int) aindex[i]]/((double)(N + N));

        for (j = 1; j <= L + L; j++) {
            allelefr[0] = allelefr[0] + (gsl_matrix_int_get(tempJuve, j, (int)
                aindex[i]) == 0 ? 1 : 0);
            Pop[j][i + 1] = gsl_matrix_int_get(tempJuve, j, (int) aindex[i]);
        }
    }
}
else {
    /* tXi[0] = 2N, so all juveniles survive */
    for (i = 0; i < N + N; i++) {

```

```

    Zbar = Zbar + Z[i]/((double)(N + N));
    for (j = 1; j ≤ L + L; j++) {
        allelefr[0] = allelefr[0] + (gsl_matrix_int_get(tempJuve, j, i) ≡ 0 ? 1 : 0);
        Pop[j][i + 1] = gsl_matrix_int_get(tempJuve, j, i + 1);
    }
}
}
return (Zbar);
}

```

This code is used in chunk 13.

## 4.5 Simulator

A discrete-time simulator for a single run.

9  $\langle$  discrete-time simulator 9  $\rangle \equiv$

```

int simulator(int N,int L,double a,double b,int Psi,double s,double
    znull,double epsilon,double *leffects,gsl_ran_discrete_t *PmXi,int
    **Pop,gsl_rng *r)
{
    /* P is the population; 2N is number of diploid individuals; L is number of
    unlinked loci; a is the skewness parameter; gamma =  $\gamma = (\gamma_1, \dots, \gamma_L)$  is the vector
    of values of locus effects. First we initialize the population P. */
    /* Pop is the current genotypes of the 2N diploid individuals; tempXi is the
    random number of juveniles per parent pair; pindex is the index of individuals
    used to form pairs; */
    int *tempXi = (int *) calloc(N + 1, sizeof(int));
    size_t *jindex = (size_t *) calloc(MAX_JUVENILES, sizeof(size_t));
    int *pindex = (int *) calloc(N + N, sizeof(int));
    gsl_matrix_int *gjuveniles = gsl_matrix_int_calloc(L + L + 1, MAX_JUVENILES + 1);
    double *traits = (double *) calloc(MAX_JUVENILES, sizeof(double));
    double *Etimes = (double *) calloc(MAX_JUVENILES, sizeof(double));
    int i, j, B, iter;
    int *allfr = (int *) calloc(1, sizeof(int));
    for (i = 1; i  $\leq$  2 * N; i++) {
        pindex[i - 1] = i;
        for (j = 1; j  $\leq$  2 * L; j++) {
            /*  $\mathbb{P}(B = 1) = \frac{1}{2}$ ; ie. we assign initial alleles with equal probability */
            B = (int) gsl_ran_bernoulli(r, .5);
            Pop[j][i] = B;
        }
    }
}

```



```

}
double zbar = 0.;
iter = 0;
for (i = 1; i ≤ 2 * N; i++) {
    for (j = 1; j ≤ L; j++) {
        zbar = zbar + (leffects[j] * (Pop[j][i] + Pop[j + L][i]));
    }
}

/* print out the initial value of the mean trait */
zbar = zbar / ((double)(N + N));
while (((iter < 100000) ∧ (fabs(zbar - znull) > epsilon))) {
    /* Pair the diploid individuals, the parents: first shuffle the index values */
    gsl_ran_shuffle(r, pindex, 2 * N, sizeof(int));
    drawXi(N, Psi, a, b, PmXi, tempXi, r);
    /* now have values of Xi for all N pairs; update population */
    zbar = juvenile_genotypes(N, L, s, znull, epsilon, Pop, pindex, tempXi, gjuveniles,
        traits, leffects, Etimes, jindex, allfr, r);
    iter = iter + 1;
    /* only need to check if all alleles are 1 */
    iter = ((allfr[0] > 0) ? iter : 1000000);
}
printf("allfr_□□%d_□□%d\n", allfr[0], iter);
/* free used memory */
free(tempXi);
free(jindex);
free(pindex);
gsl_matrix_int_free(gjuveniles);

```

```
free(allfr);  
free(traits);  
free(Etimes);  
    /* return the count of generations needed to reach optimum */  
return (iter);  
}
```

This code is used in chunk 13.

## 4.6 many runs

Generate many replicates and the time, number of generations, to optimum.

10  $\langle$ many runs 10 $\rangle \equiv$

```
void replicates(int N, int L, double a, double b, int psi, double seleccoeff, double
    znull, double epsilon, int nruns, double *loceffects, gsl_rng * r, char
    skra[200])
{
    double *PXi = (double *) calloc(1 + psi, sizeof(double));
    int **mPop = alloc_2d_array(L, N);
    int k;
    double mean = 0.;
    for (k = 0; k ≤ psi; k++) {
        PXi[k] = (a > 0. ? pow(b, a) * (pow(1./(((double) k) + b),
            a) - (k < psi ? pow(1./(((double)(1 + k)) + b), a) : 0.)) : 1.);
        assert(PXi[k] ≥ 0.);
        mean = mean + (((double) k) * PXi[k]);
    }
    assert(mean ≥ 2.);
    gsl_ran_discrete_t * Pmass = gsl_ran_discrete_preproc(1 + psi, PXi);
    FILE *f = fopen(skra, "w");
    int rep, svar;
    for (rep = 0; rep < nruns; rep++) {
        svar = simulator(N, L, a, b, psi, seleccoeff, znull, epsilon, loceffects, Pmass, mPop, r);
        fprintf(f, "%d\n", svar);
        printf("%d\n", rep);
    }
}
```

```
free(PXi);  
gsl_ran_discrete_free(Pmass);  
fclose(f);  
free_2d_array(mPop, L);  
}
```

This code is used in chunk 13.

## 4.7 Allocate a 2d array

Allocate a 2d array; use it for large population size.

11  $\langle$  allocate array 11  $\rangle \equiv$

```
int **alloc_2d_array(int rows, int cols)
{
    int **m =  $\Lambda$ ;
    m = (int **) calloc(rows + rows + 1, sizeof(int *));
    int i;
    for (i = 0; i  $\leq$  rows + rows; i++) {
        m[i] = (int *) calloc(cols + cols + 1, sizeof(int));
    }
    return (m);
}
```

This code is used in chunk 13.

## 4.8 Free a 2d array

Free a 2d array.

12  $\langle$  free 2d array 12  $\rangle \equiv$

```
void free_2d_array(int **a, int n)
{
    int i;
    for (i = 0; i  $\leq$  n + n; i++) {
        free(a[i]);
    }
    free(a);
    a =  $\Lambda$ ;
}
```

This code is used in chunk 13.

## 4.9 the *main* function

13 <Includes 15>

<print matrix 14>

<allocate array 11>

<free 2d array 12>

<random number generator 5>

<object definitions 6>

<initialize distribution for  $X_i$  7>

<assign juvenile genotypes 8>

<discrete-time simulator 9>

<many runs 10>

```
int main(int argc, char *argv[])
{
    initialise the random number generator

    setup_rng((unsigned long int) atoi(argv[10]));

    double *leffects = (double *) calloc(atoi(argv[2]) + 1, sizeof(double));

    int ell;

    for (ell = 1; ell ≤ atoi(argv[2]); ell++) {
        leffects[ell] = 1.;
    }

    leffects[1] = 1.;

    replicates(atoi(argv[1]), atoi(argv[2]), atof(argv[3]), atof(argv[4]), atoi(argv[5]),
               atof(argv[6]), atof(argv[7]), atof(argv[8]), atoi(argv[9]), leffects, rngtype,
               argv[11]);

    // clear all used memory:

    gsl_rng_free(rngtype);
```

```
free(leffects);  
return GSL_SUCCESS;  
end of main function  
}
```



## 4.10 Print a GSL integer matrix

print matrix

14  $\langle$ print matrix 14 $\rangle \equiv$

```
void printmatrix(int rows, int cols, gsl_matrix_int * m)
{
    int i, j;
    for (i = 1; i ≤ rows; i++) {
        for (j = 1; j ≤ cols; j++) {
            printf("%d□", gsl_matrix_int_get(m, i, j));
        }
        printf("\n");
    }
}
```

This code is used in chunk 13.

## 5 Includes

15 ⟨Includes 15⟩ ≡

```
#include <stdio.h>
#include <stdlib.h>
#include <math.h>
#include <gsl/gsl_rng.h>
#include <gsl/gsl_randist.h>
#include <gsl/gsl_vector.h>
#include <gsl/gsl_matrix.h>
#include <gsl/gsl_sf_pow_int.h>
#include <gsl/gsl_errno.h>
#include <gsl/gsl_sf_elementary.h>
#include <gsl/gsl_sf_gamma.h>
#include <gsl/gsl_fit.h>
#include <gsl/gsl_multifit_nlin.h>
#include <gsl/gsl_integration.h>
#include <gsl/gsl_sf_exp.h>
#include <gsl/gsl_sf_log.h>
#include <gsl/gsl_sf_expint.h>
#include <gsl/gsl_combination.h>
#include <gsl/gsl_linalg.h>
#include <gsl/gsl_combination.h>
#include <gsl/gsl_statistics_double.h>
#include <gsl/gsl_statistics_int.h>
#include <gsl/gsl_sort.h>
#include <assert.h>
```

This code is used in chunk 13.

## 6 Funding

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(<https://dfg-spp1819.uni-hohenheim.de/105254?L=1>). The generous support of Museum für Naturkunde in Berlin is warmly acknowledged.

## 7 References

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