Disentangling how ***selection***, ***demography***, *and* ***sex-biased behavior*** *influence* ***genetic diversity*** *using field study–informed* ***genetic simulations***

MAX PLANCK INSTITUTE
FOR EVOLUTIONARY ANTHROPOLOGY

AgroParisTech

Timothé Dandoy

I. Introduction

Genetic Diversity

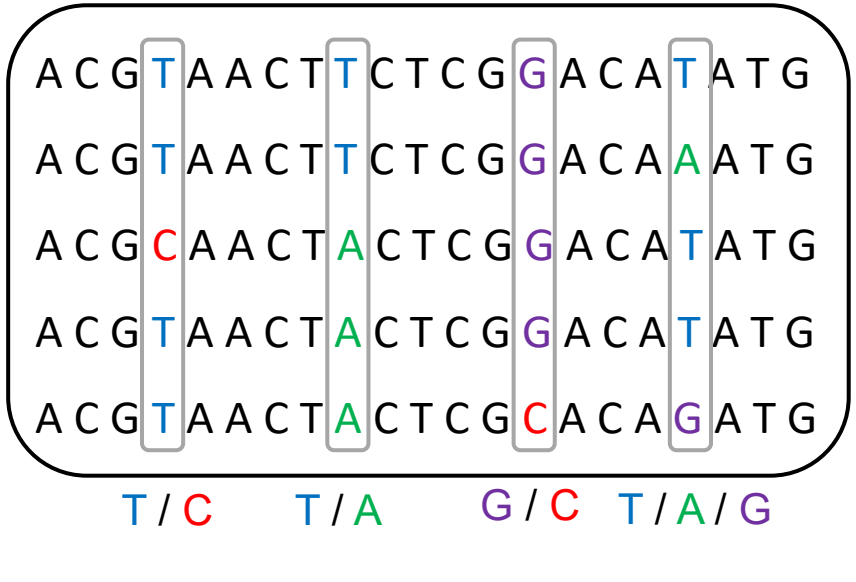
=> Measure of all the differences found in genomes of a species or a population

- **Nucleotide diversity** π : average number of nucleotide differences per site within a sequence in a population

$$\pi = 2\frac{\sum_{i<j} k_{ij}}{n(n-1)}$$

n: number of sequences sampled

k_{ij} *: number of nucleotide differences between ith and jth sequences*



$\Rightarrow \pi = 2{,}1$

Molecular Population Genetics, Hahn (2019)

Genetic Diversity

- **Expected Value** : $\pi = 4 * Ne * \mu$

Ne : Effective Population size
μ : Mutations Rate

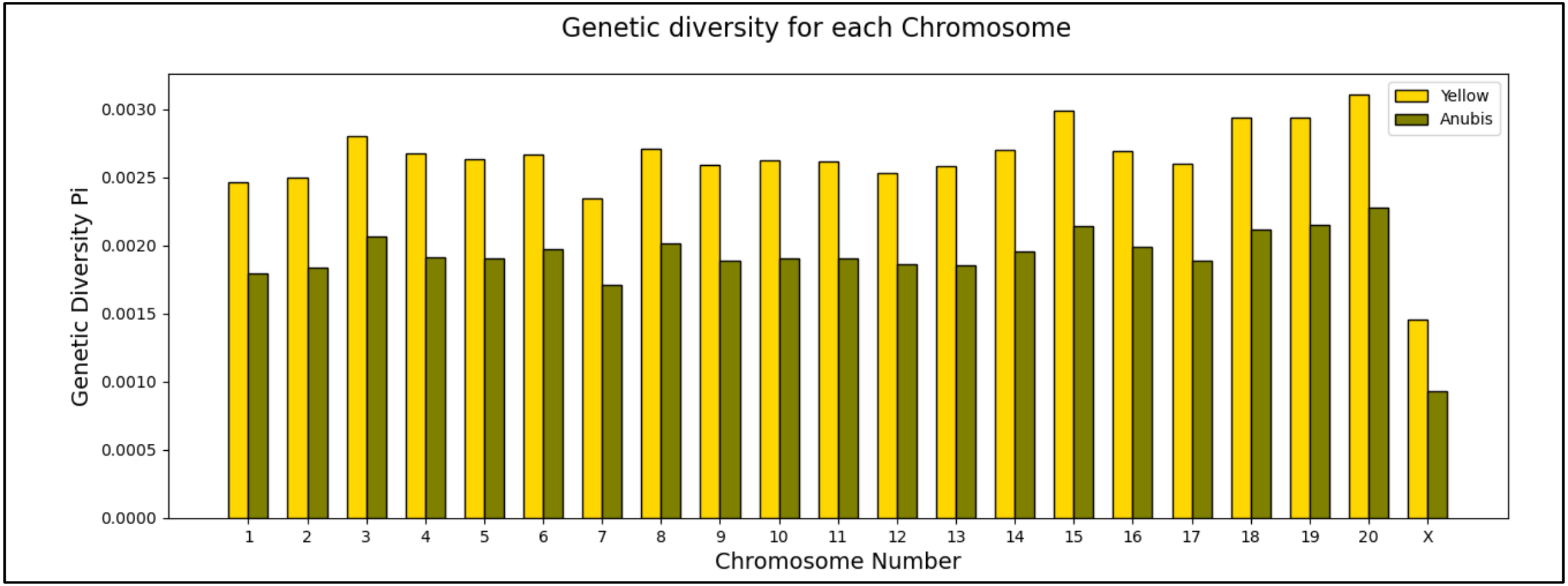
- $Ne_X = 0.75 * Ne_A$ with Sex-ratio = 0.5

=> X-to-A ratio = $\pi_X / \pi_A = 0.75$ under assumption of:

Panmixia
Sex-ratio = 0.5
No selection

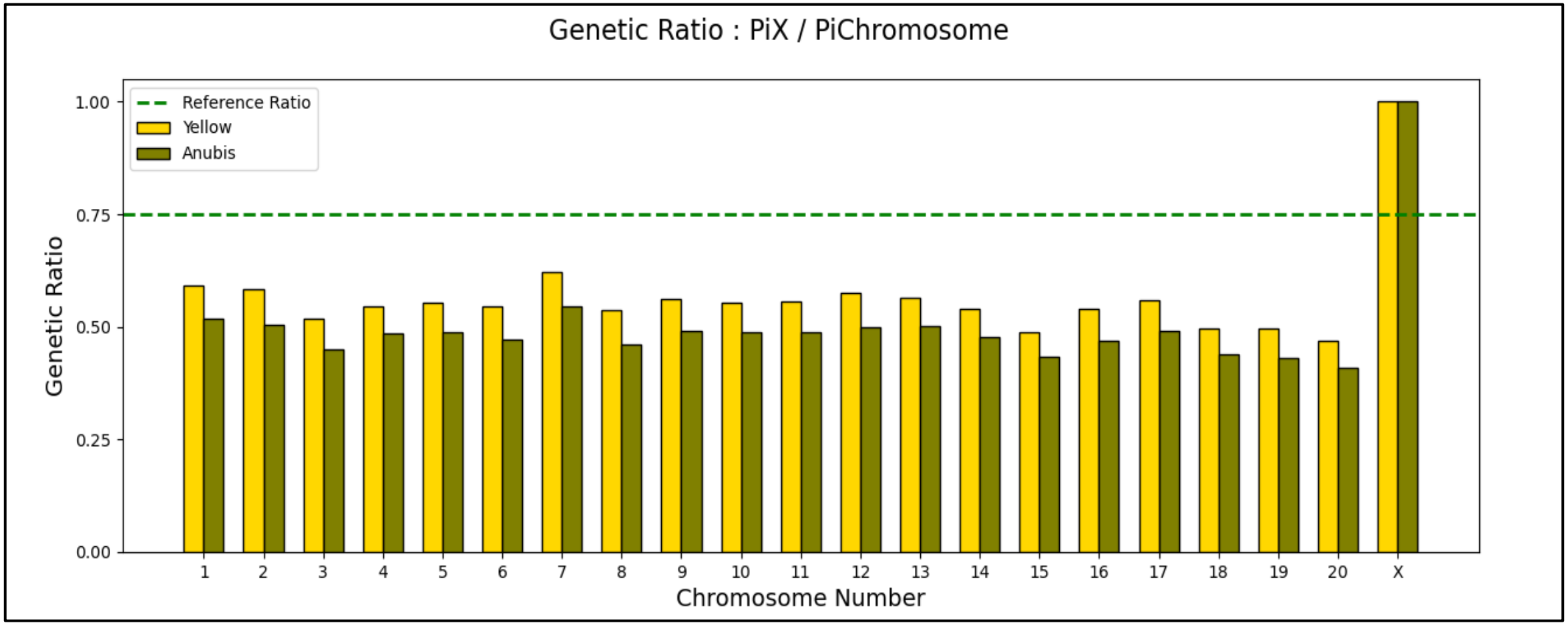
Molecular Population Genetics, Hahn (2019)

Genetic Diversity in Baboons



=> The X-to-A genetic ratio is below the expectation

Genetic X-to-A Ratio in Baboons



=> The X-to-A genetic ratio is below the expectation

What forces or processus may influence the X-to-A ratio of a population ?

Amboseli Baboon Data

Safaripedia.com

Amboseli Baboons (*Papio cynocephalus*)

Elizabeth Archie's photo

Demographic and Behavioral Data

Genetic Data

Elizabeth Archie's photo

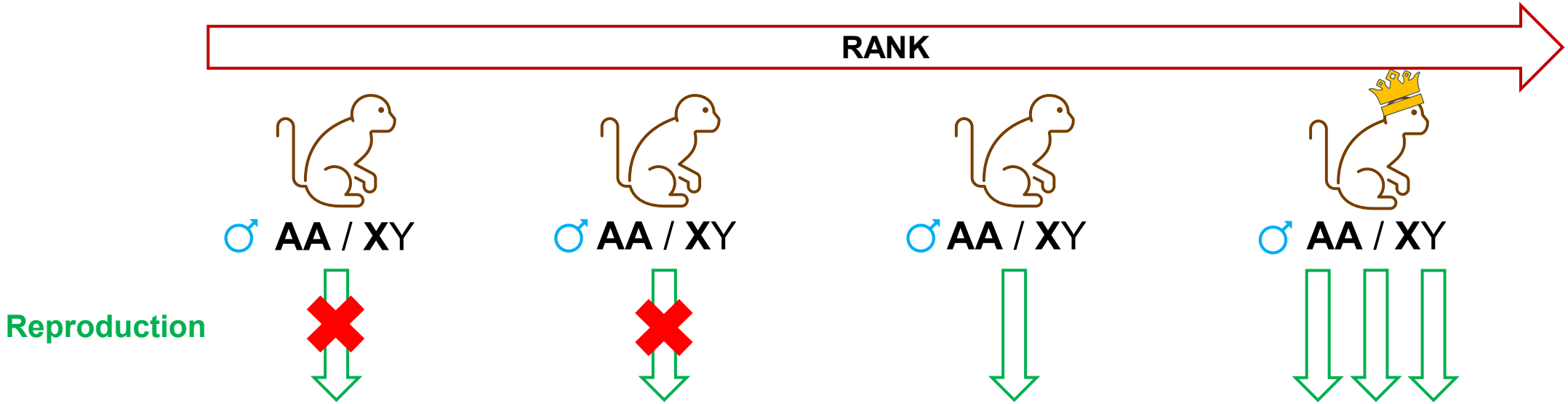
The Amboseli Baboon Research Project: 40 Years of Continuity and Change, Alberts & Altmann (2012)

Sex-biased behaviors

Reproductive Tactics of Male Savanna Baboons, Noë & Sluijter (1990)

Differential impact on the Autosomal (A) diversity and the Chromosome X diversity

Ex **Males Reproductive Skew**:



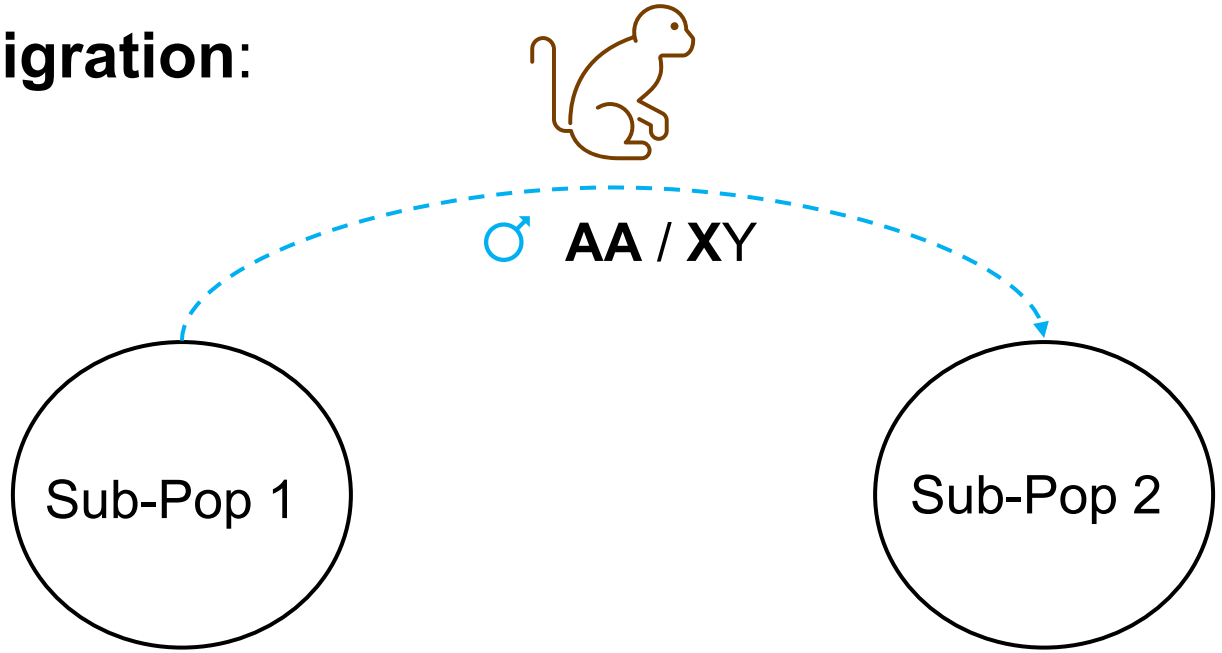
=> The X-to-A genetic ratio increases

Sex-biased behaviors

Balancing Costs and Opportunities: Dispersal in Male Baboons, Alberts & Altmann (1995)

Differential impact on the Autosomal (A) diversity and the Chromosome X diversity

Ex **Male-Only Migration**:



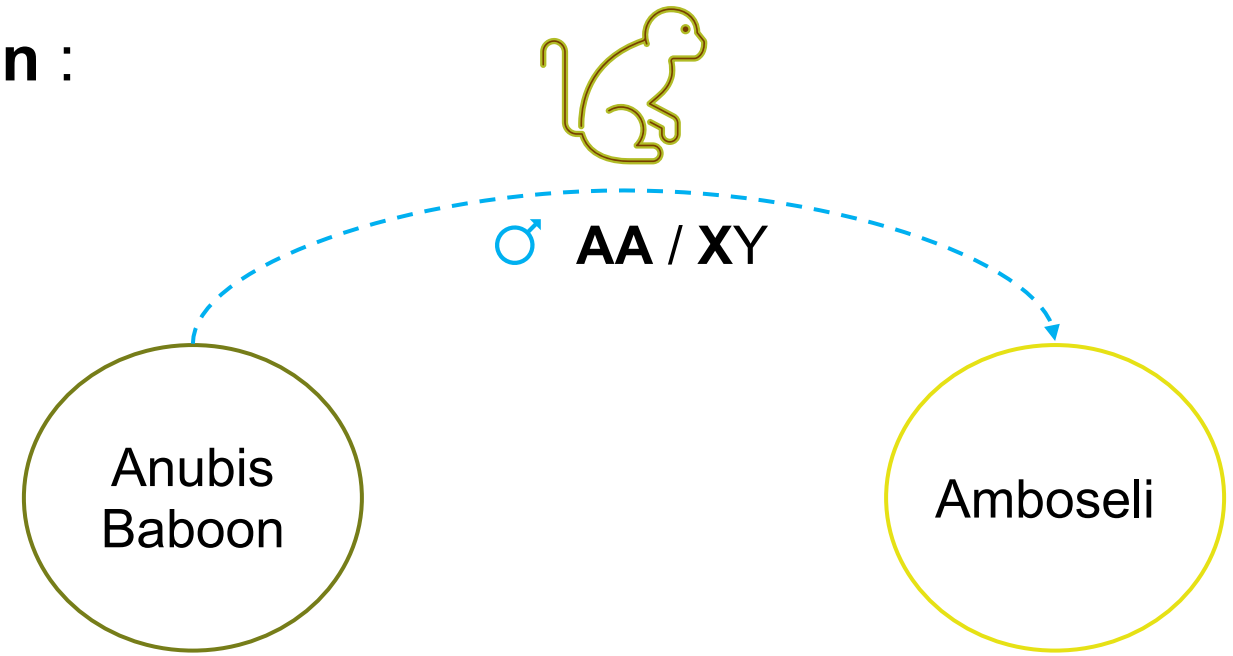
=> The X-to-A genetic ratio decreases

Sex-biased Process

The Amboseli Baboon Research Project: 40 Years of Continuity and Change, Alberts & Altmann (2012)

Differential impact on the Autosomal (A) diversity and the Chromosome X diversity

Ex **Hybridization** :



=> The X-to-A genetic ratio decreases

Genetic Forces

- **Selection**

  Haploidy of X in males

- **Hybridization** between Anubis and Yellow baboons

  Haldane's Rule : reproduction and hybridization incompatibilities accumulate faster on X

Comparative studies on speciation: 30 years since Coyne and Orr, Matute & Cooper (2021)

=> **Stronger** selection effect **on the X Chromosome** than on the Autosomes

=> The X-to-A genetic ratio decreases

Amboseli Baboon

Elizabeth Archie's photo

Objectives

Computational Simulations to model :

- Reproductive Skew in Males
- Male-Only Migration
- Hybridization

} Sex-biased

- Selection

Objectives

Assess the strength of each forces on the X-to-A ratio

Determine if sex-biased processes enough for explaining the difference in genetic diversity between the X and the autosomes, or whether instead we need to invoke natural selection

II. Methods

A. SLiM Presentation

SLiM Presentation

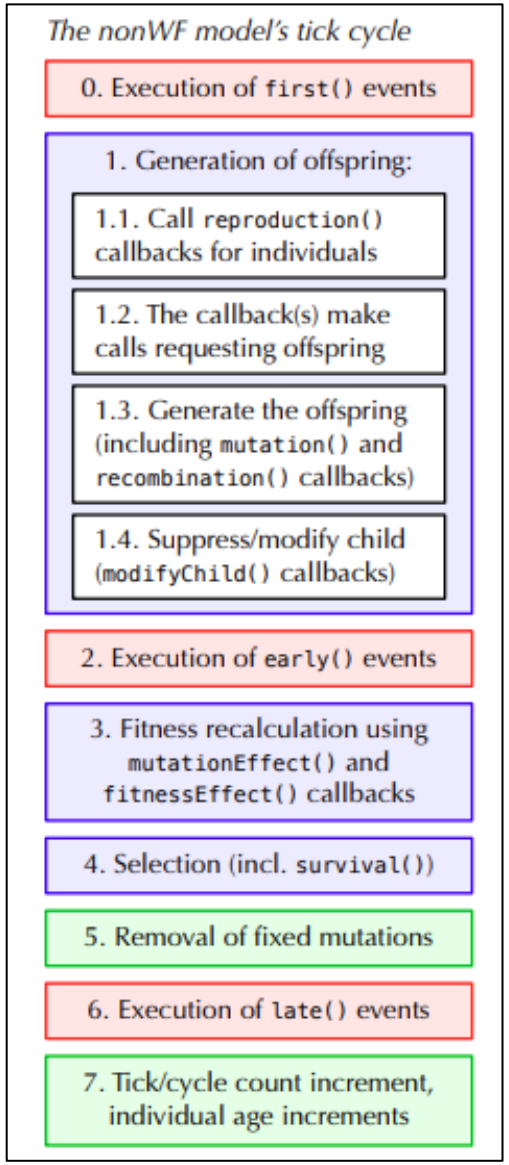
SLiM

Evolutionary simulation framework that combines a powerful engine for population genetic simulations with the capability of modeling arbitrarily complex evolutionary scenarios

=> Forward simulation of both Dynamics and Genetics of the population

Simulations through the Ticks (1 Tick = 1 Year)

Each individual -> 1 pair of A + 1 pair of sex-chromosomes



SLiM Manual

SLiM Presentation

SLiM

500 individuals
10 subpopulations
Chromosomes length = 1e7
Mutations Rates = 1,25e-8

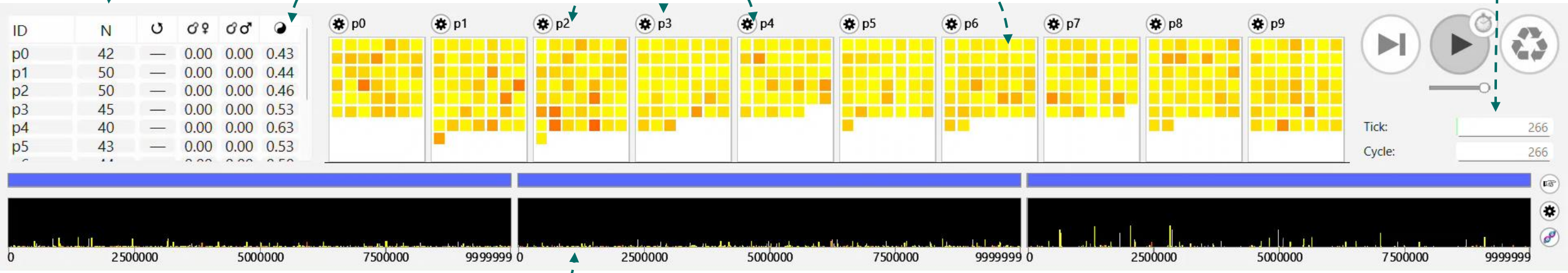
Populations size

Sex ratio

Subpopulations

Individuals

Ticks



Mutations frequencies

Autosomes

X Chromosomes

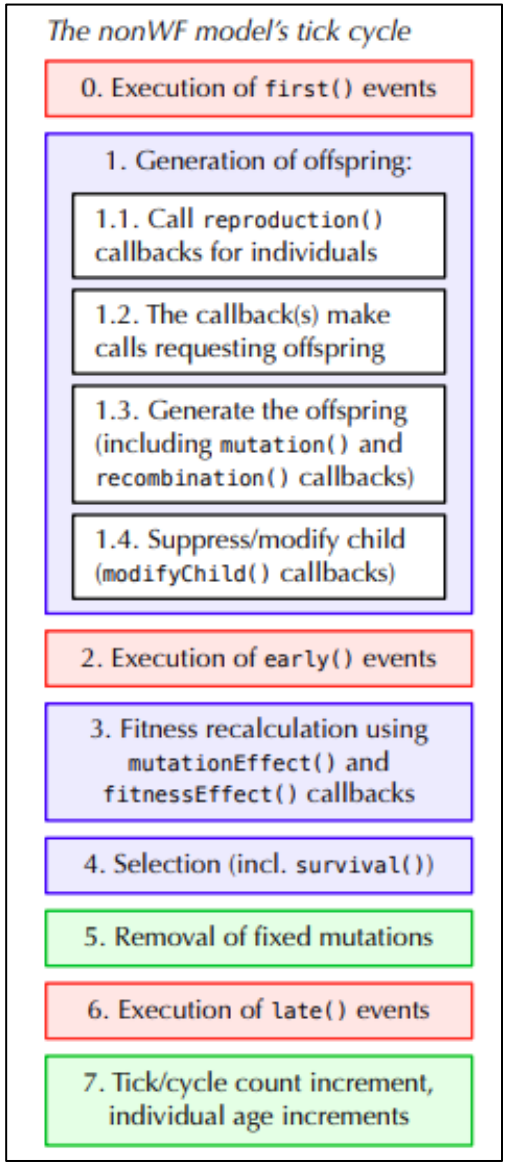
Y Chromosomes

B. Reference Models

Reference Models

Global Parameters:

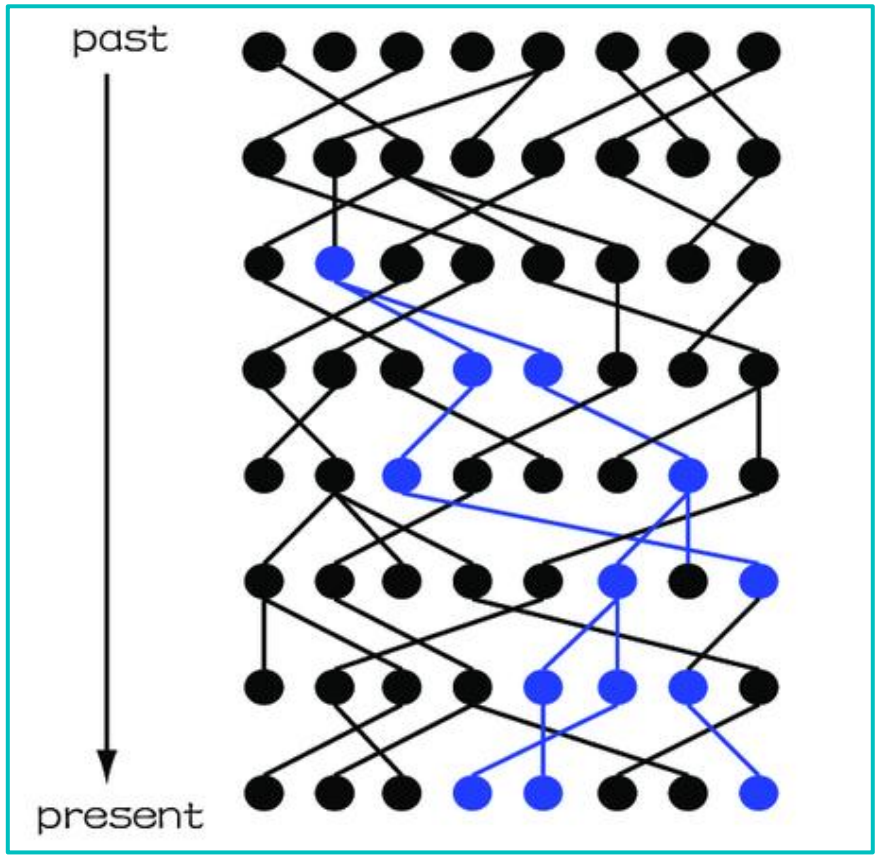
- Population size : **750 Individuals**
- Sex Ratio : **0,5 (male proportion)**
- **1 Offsprings per Reproduction**
- **1 pair of Autosomes** and **1 pair of sex Chromosomes**
- Chromosomes Length : **1e8 nucleotides**
- Mutations Rate : **5e-7 mut.nuceotide^{-1}.tick^{-1}**
- Only **Neutral Mutations**
- Recombination Rate : **4e-7 recomb.chr^{-1}.gamete^{-1}.tick^{-1}**
- Simulations Time : **2e4 Ticks**



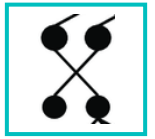
SLiM Manual

Reference Models

Wright-Fisher Model (WF)



Liu, Xiaomo (2005)



Non-Overlapping generations

Constant Population Size, Constant Sex Ratio

Random mating between a male and a female

No selection

Reference Models

Non-Wright-Fisher Models (NWF) :

-> Overlapping generations
=> Individuals may survive multiple years

-> Average Population Size and average Sex Ratio are constant
=> Carrying Capacity

-> 3 different Reproduction Systems :

Reference Models

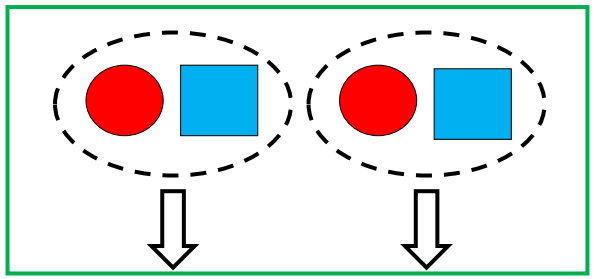
Non-Wright-Fisher Models (NWF) :

-> Non-Overlapping generations
=> Individuals may survive multiple years

-> Average Population Size and average Sex Ratio are constant
=> Carrying Capacity

-> 3 different Reproduction Systems :

NWF Vanilla (NWF_V):



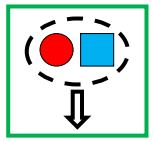
Reference Models

Non-Wright-Fisher Models (NWF) :

-> Non-Overlapping generations
=> Individuals may survive multiple years

-> Average Population Size and average Sex Ratio are constant
=> Carrying Capacity

-> 3 different Reproduction Systems :



NWF Vanilla (NWF_V):

Each Year,

- Formations of male-female couple

=> males and females reproduce once a year in maximum

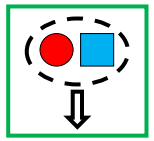
Reference Models

Non-Wright-Fisher Models (NWF) :

-> Non-Overlapping generations
=> Individuals may survive multiple years

-> Average Population Size and average Sex Ratio are constant
=> Carrying Capacity

-> 3 different Reproduction Systems :



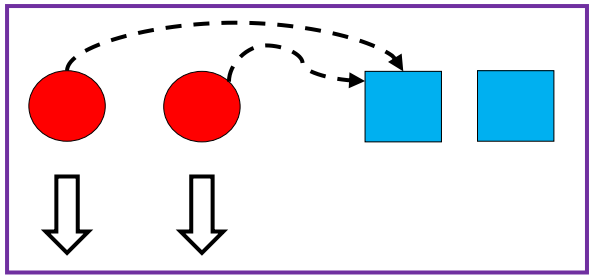
NWF Vanilla (NWF_V):

Each Year,

- Formations of male-female couple

=> males and females reproduce once a year in maximum

NWF Female Choice (NWF_FC):



Reference Models

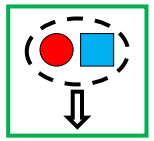
Non-Wright-Fisher Models (NWF) :

-> Non-Overlapping generations
=> Individuals may survive multiple years

-> Average Population Size and average Sex Ratio are constant
=> Carrying Capacity

-> 3 different Reproduction Systems :

NWF Vanilla (NWF_V):

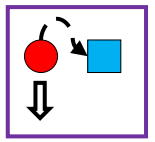


Each Year,

- Formations of male-female couple

=> males and females reproduce once a year in maximum

NWF Female Choice (NWF_FC):



- All female reproduce once a year

- They choose their male randomly among the population

=> males can reproduce several times a year

Reference Models

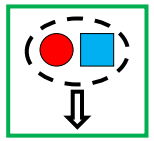
Non-Wright-Fisher Models (NWF) :

-> Non-Overlapping generations
=> Individuals may survive multiple years

-> Average Population Size and average Sex Ratio are constant
=> Carrying Capacity

-> 3 different Reproduction Systems :

NWF Vanilla (NWF_V):

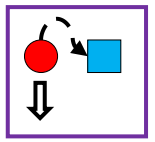


Each Year,

- Formations of male-female couple

=> males and females reproduce once a year in maximum

NWF Female Choice (NWF_FC):

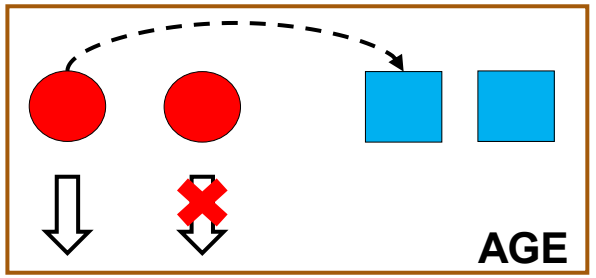


- All female reproduce once a year

- They choose their male randomly among the population

=> males can reproduce several times a year

NWF Life Table (NWF_LT):



Reference Models

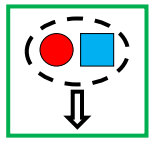
Non-Wright-Fisher Models (NWF) :

-> Non-Overlapping generations
=> Individuals may survive multiple years

-> Average Population Size and average Sex Ratio are constant
=> Carrying Capacity

-> 3 different Reproduction Systems :

NWF Vanilla (NWF_V):

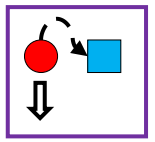


Each Year,

- Formations of male-female couple

=> males and females reproduce once a year in maximum

NWF Female Choice (NWF_FC):

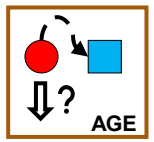


- All female reproduce once a year

- They choose their male randomly among the population

=> males can reproduce several times a year

NWF Life Table (NWF_LT):



Same as Female Choice, except the addition of an age structure:

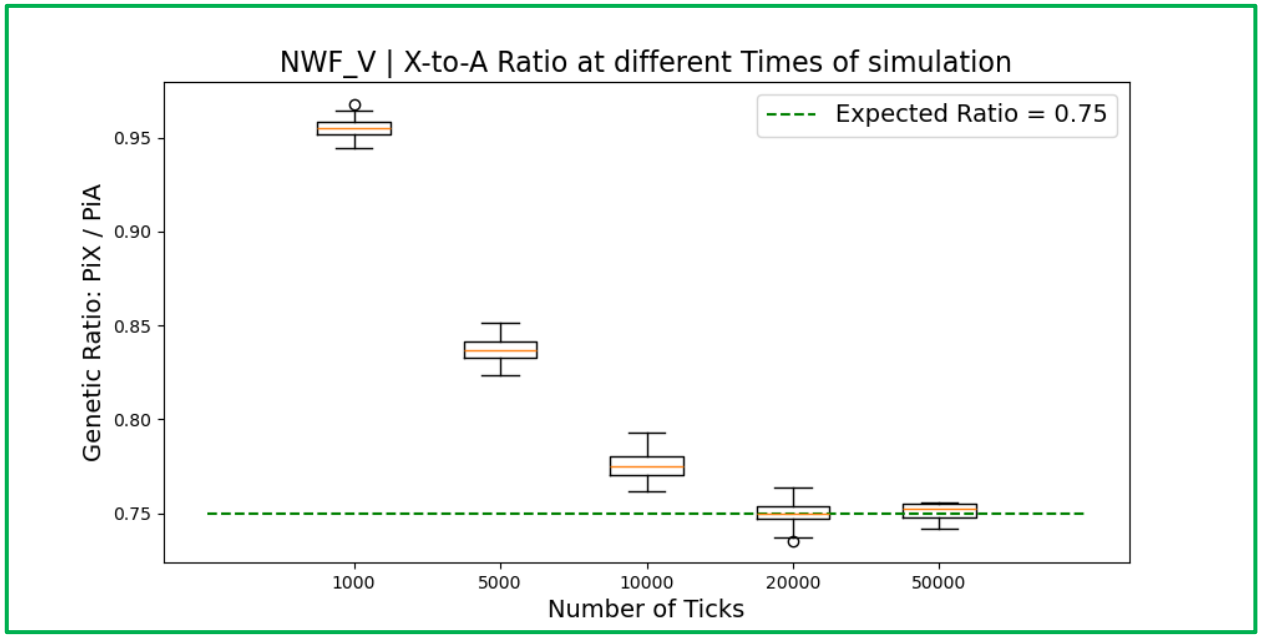
- a mortality table (♂ & ♀)

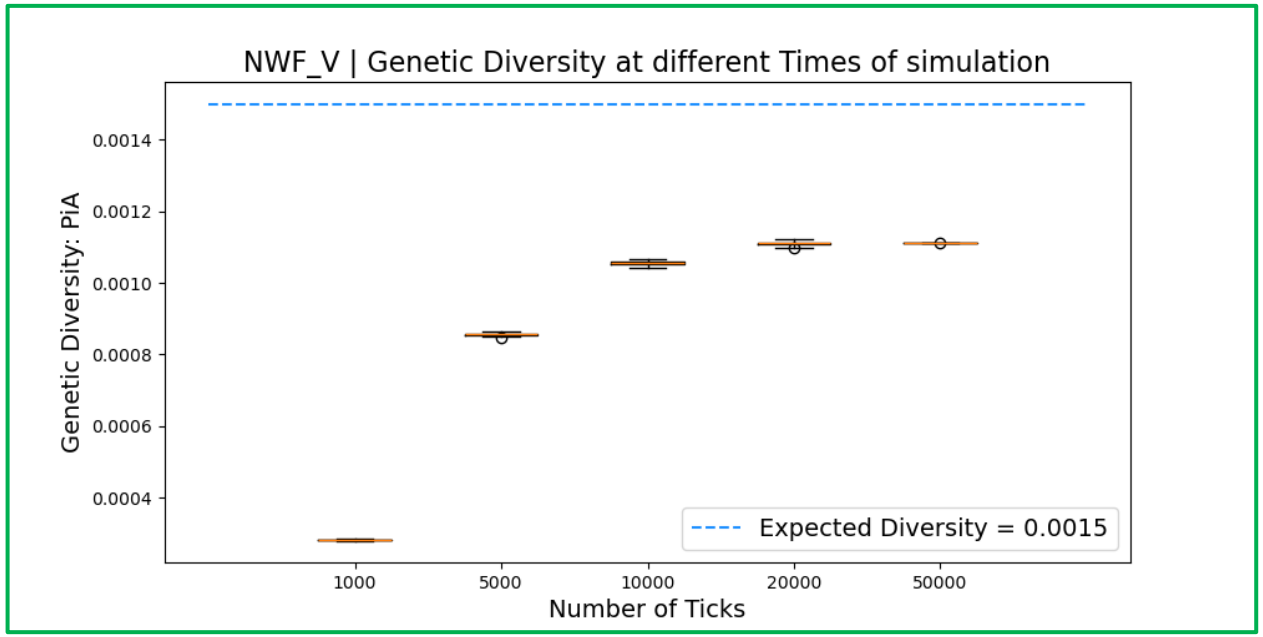
- a fertility table (♀)

=> female may not reproduce every years

C. Models Validation

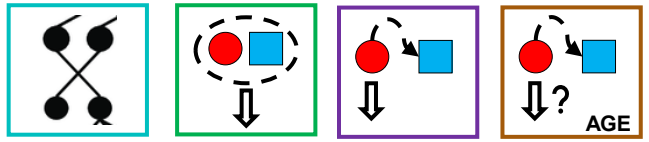
Burn-in Period NWF_V

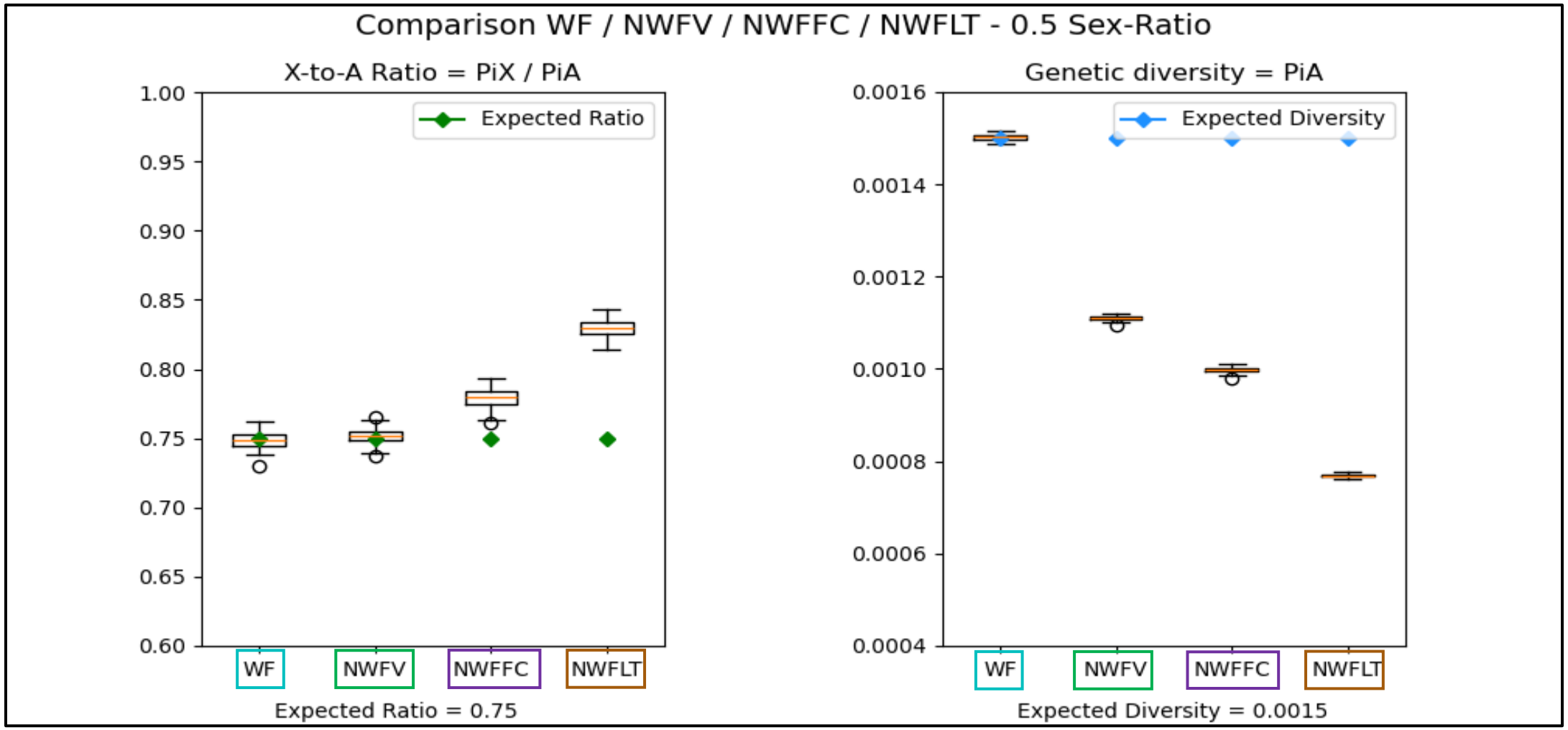




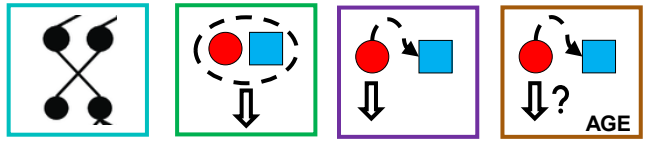
=> Simulations must last 20000 Ticks

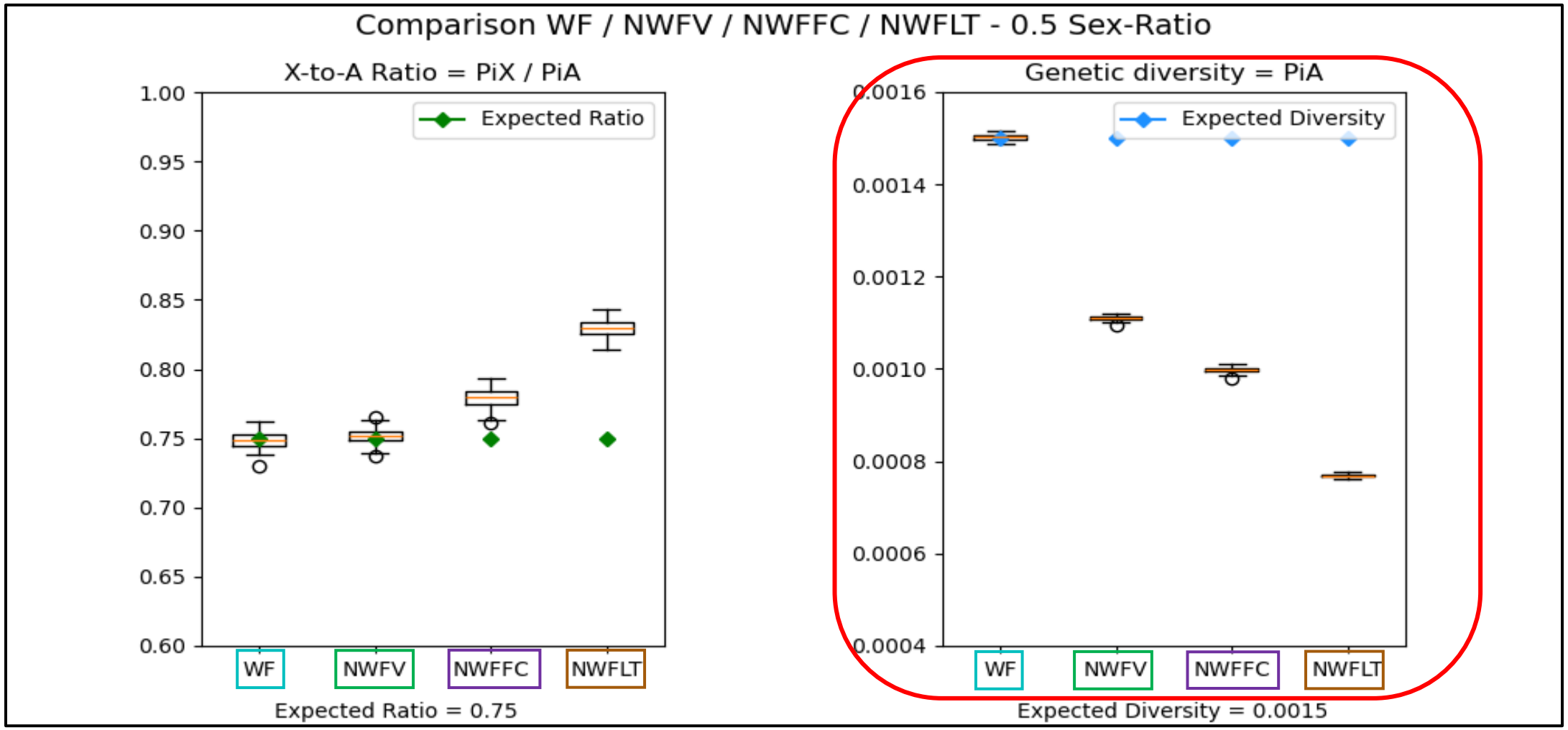
Diversity Estimations





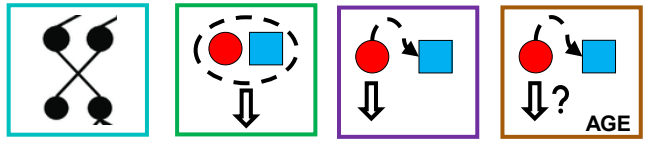
Diversity Estimations

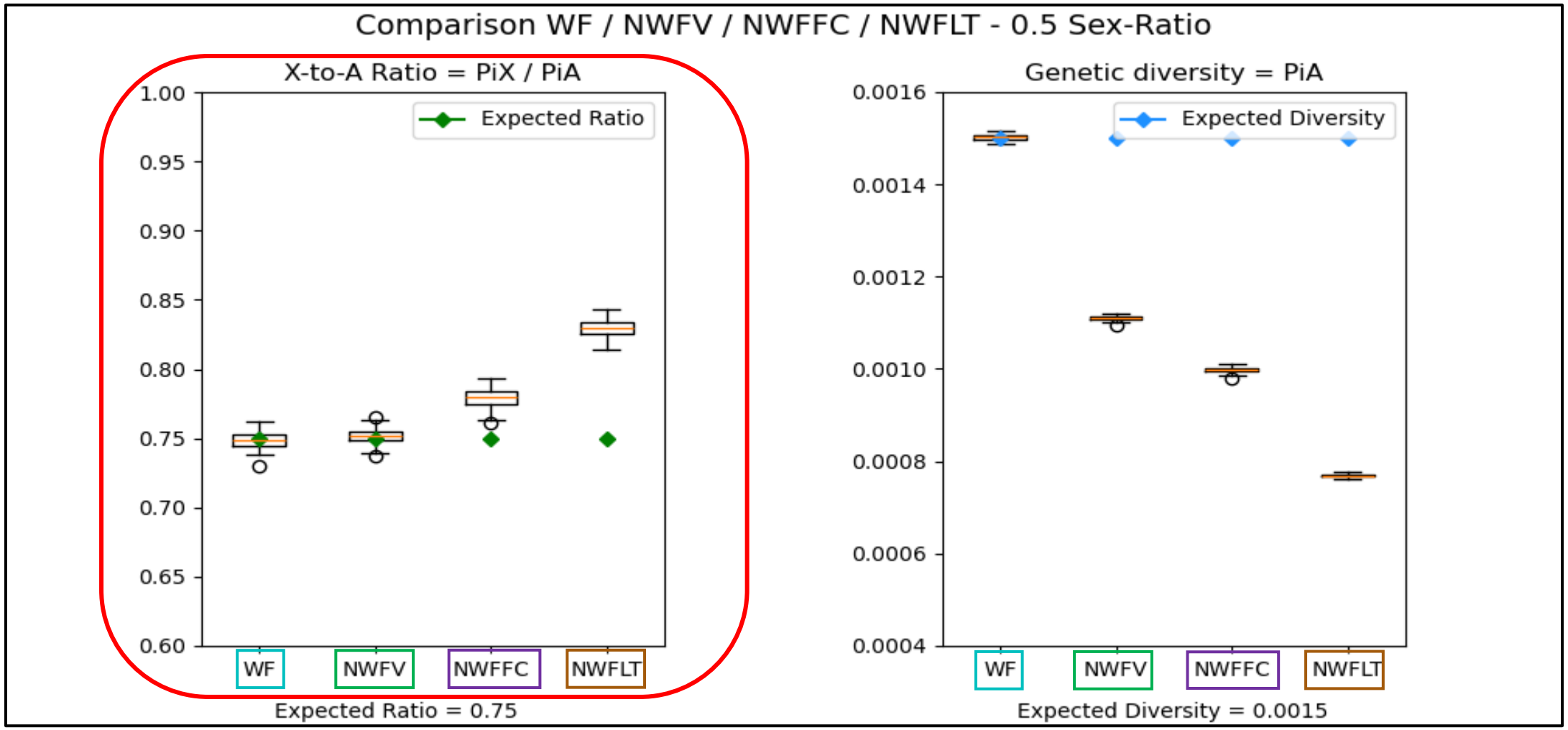




=> Genetic Diversity is reduced in NWF models

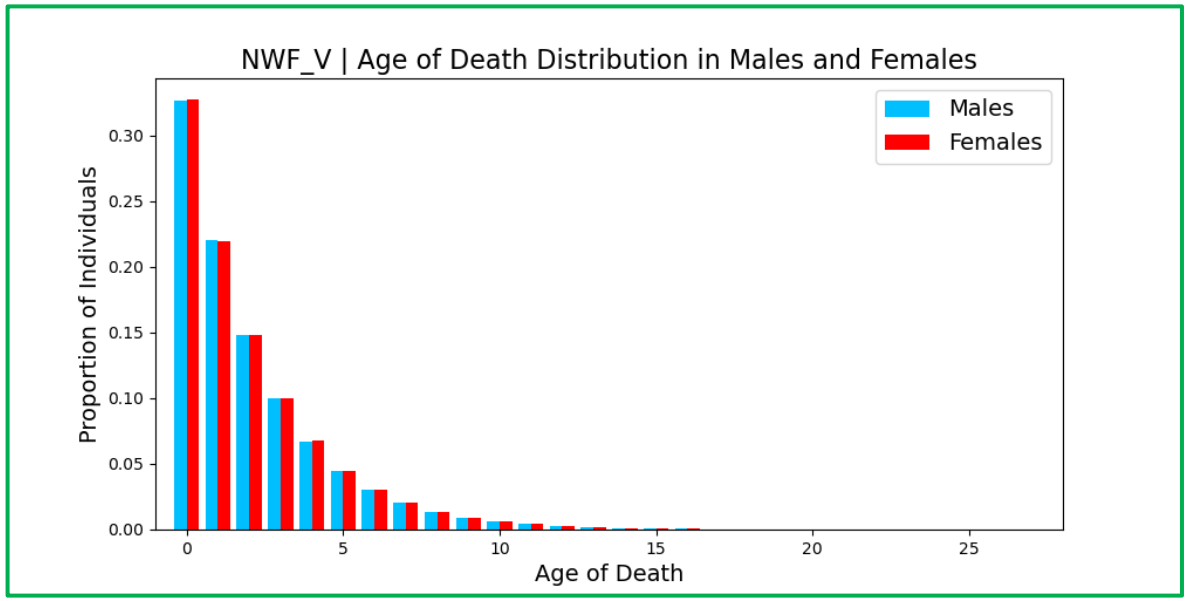
Diversity Estimations

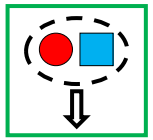


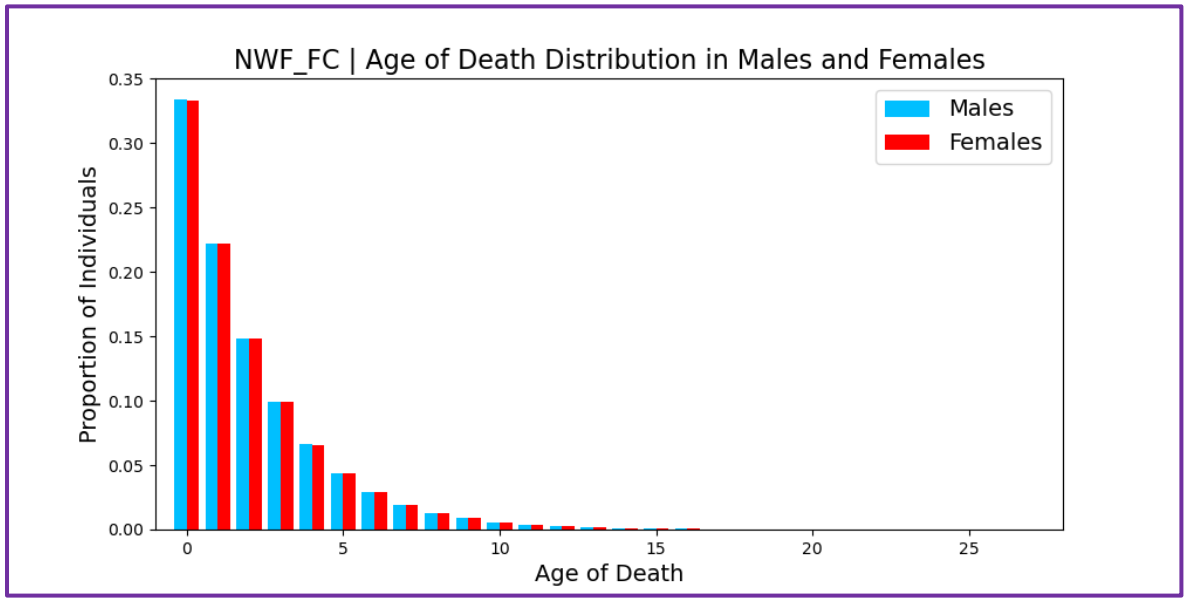


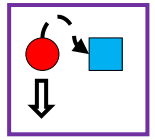
=> Higer ratio for NWF_FC and NWF_LT ?

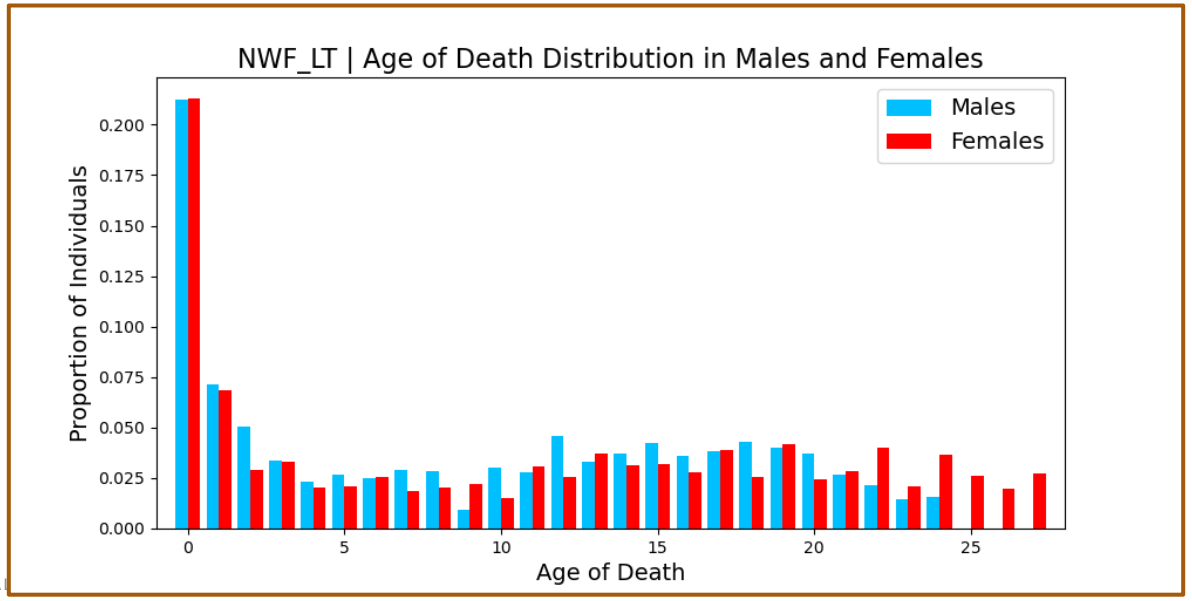
Age of Death

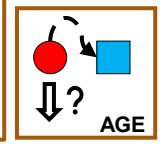

NWF_V | Age of Death Distribution in Males and Females
Males
Females
Proportion of Individuals
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0
5
10
15
20
25
Age of Death



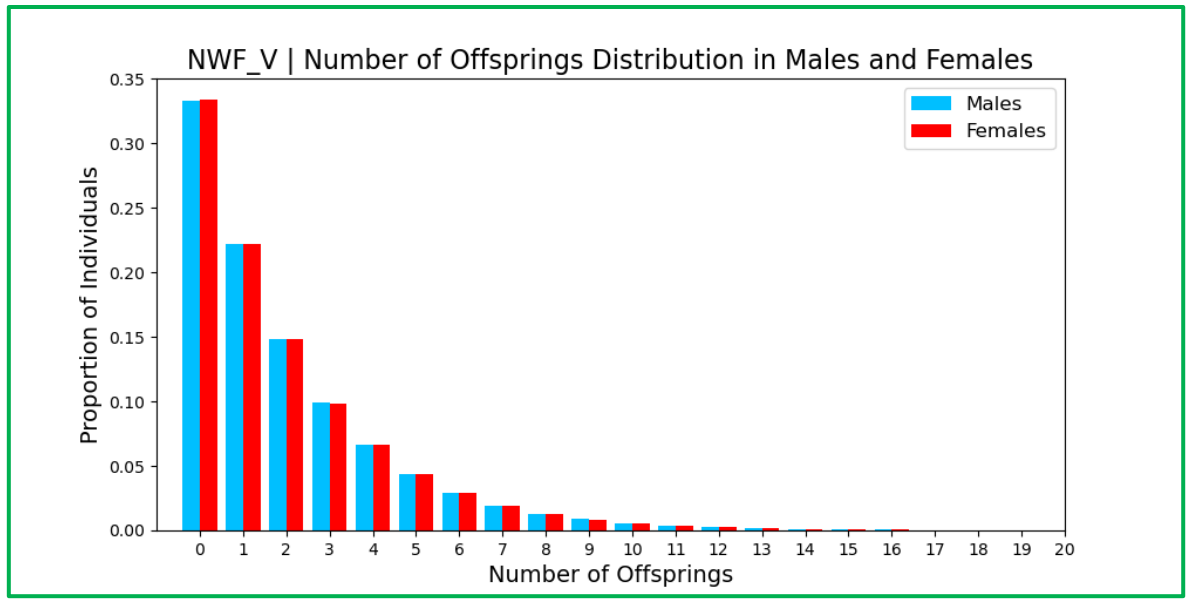

NWF_FC | Age of Death Distribution in Males and Females
Males
Females
Proportion of Individuals
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0
5
10
15
20
25
Age of Death

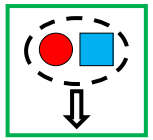


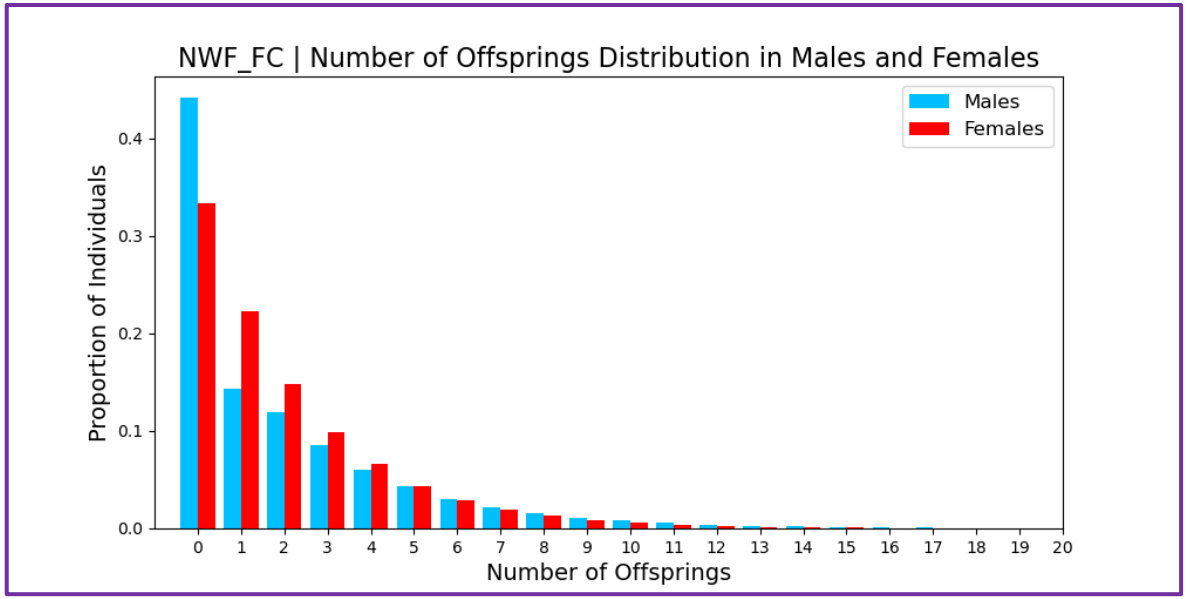

NWF_LT | Age of Death Distribution in Males and Females
Males
Females
Proportion of Individuals
0.000
0.025
0.050
0.075
0.100
0.125
0.150
0.175
0.200
0
5
10
15
20
25
Age of Death

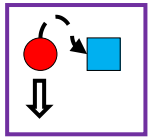

?
AGE

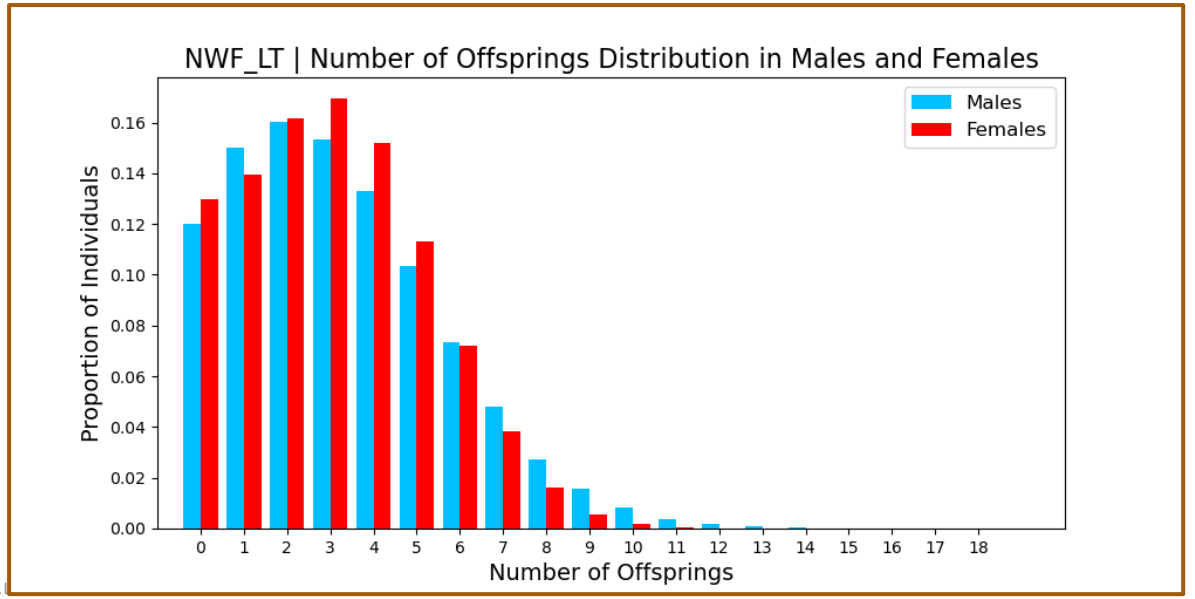
Number of Offsprings

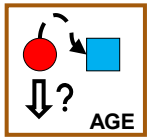












Intrinsic Reproductive Skew

N : Number of sampled individuals
R : Total number of Offsprings of all the individuals
T : Total time of exposure of all the individuals
r : Number of offsprings of every individual
t : Time of exposure of every individual

Reproductive Skew estimator :

The multinomial index: a robust measure of reproductive skew, Ross (2020)

$$M(r,t) = \breve{M}(r, t) - E\left[\breve{M}(X, t)\right]$$

$$\breve{M}(r,t) = \frac{N}{R^2}\sum_{i=1}^{N}(ri - \bar{ri})^2$$

$$X \sim Multinomial\left(R, \frac{t}{T}\right)$$

Reproductive Skew of males and females for each NWF models

	Males	Females	Maximum	Minimum
NWFV	-0.487533	-0.465266	5044	-0.506629
NWFFC	-0.000159	-0.496887	4937	-0.499141
NWFLT	-0.000880	-0.077242	3271	-0.325602

Intrinsic Reproductive Skew

N : Number of sampled individuals
R : Total number of Offsprings of all the individuals
T : Total time of exposure of all the individuals
r : Number of offsprings of 1 individual
t : Time of exposure of 1 individual

Reproductive Skew estimator :

The multinomial index: a robust measure of reproductive skew, Ross (2020)

$$M(r,t) = \breve{M}(r, t) - E\left[\breve{M}(X, t)\right]$$

$$\breve{M}(r,t) = \frac{N}{R^2}\sum_{i=1}^{N}(ri - \bar{ri})^2$$

$$X \sim Multinomial\left(R, \frac{t}{T}\right)$$

Reproductive Skew of males and females for each NWF models

	Males	Females	Maximum	Minimum
NWFV	-0.487533	-0.465266	5044	-0.506629
NWFFC	-0.000159	-0.496887	4937	-0.499141
NWFLT	-0.000880	-0.077242	3271	-0.325602

Low variance Distribution

Intrinsic Reproductive Skew

N : Number of sampled individuals
R : Total number of Offsprings of all the individuals
T : Total time of exposure of all the individuals
r : Number of offsprings of 1 individual
t : Time of exposure of 1 individual

Reproductive Skew estimator :

The multinomial index: a robust measure of reproductive skew, Ross (2020)

$$M(r,t) = \breve{M}(r, t) - E\left[\breve{M}(X, t)\right]$$

$$\breve{M}(r,t) = \frac{N}{R^2}\sum_{i=1}^{N}(ri - \bar{ri})^2$$

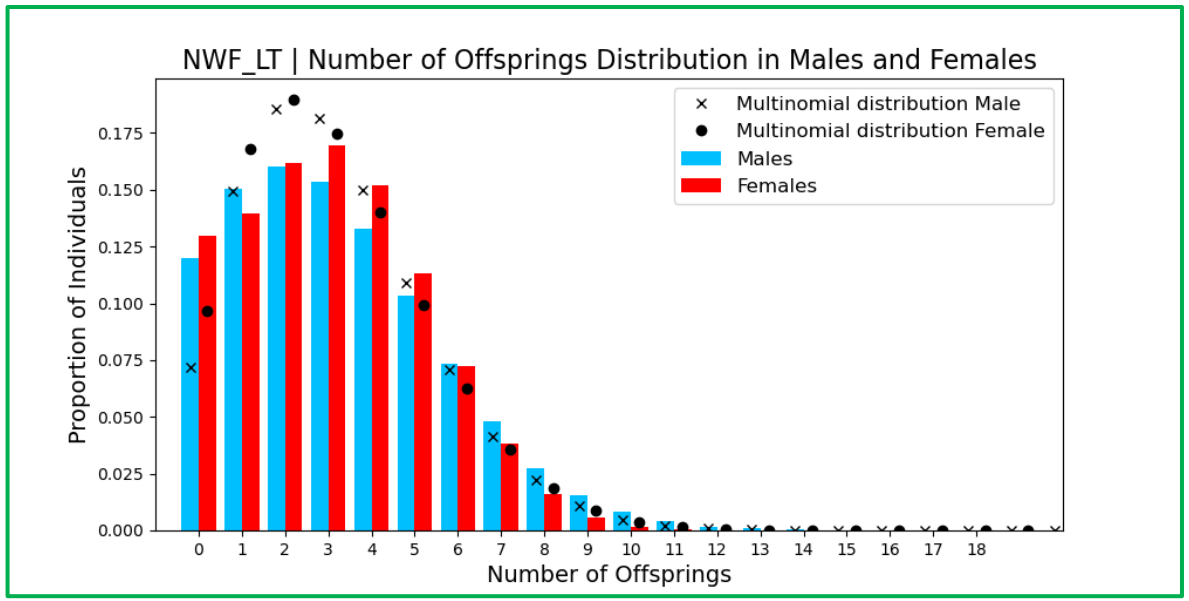
$$X \sim Multinomial\left(R, \frac{t}{T}\right)$$

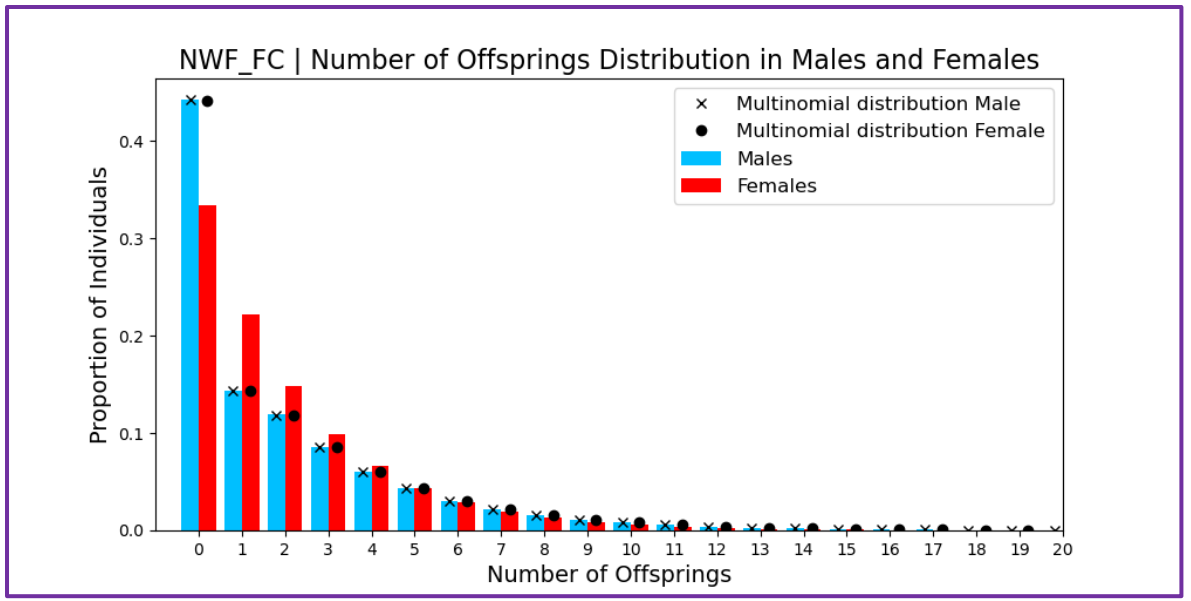
Reproductive Skew of males and females for each NWF models

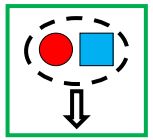
	Males	Females	Maximum	Minimum
NWFV	-0.487533	-0.465266	5044	-0.506629
NWFFC	-0.000159	-0.496887	4937	-0.499141
NWFLT	-0.000880	-0.077242	3271	-0.325602

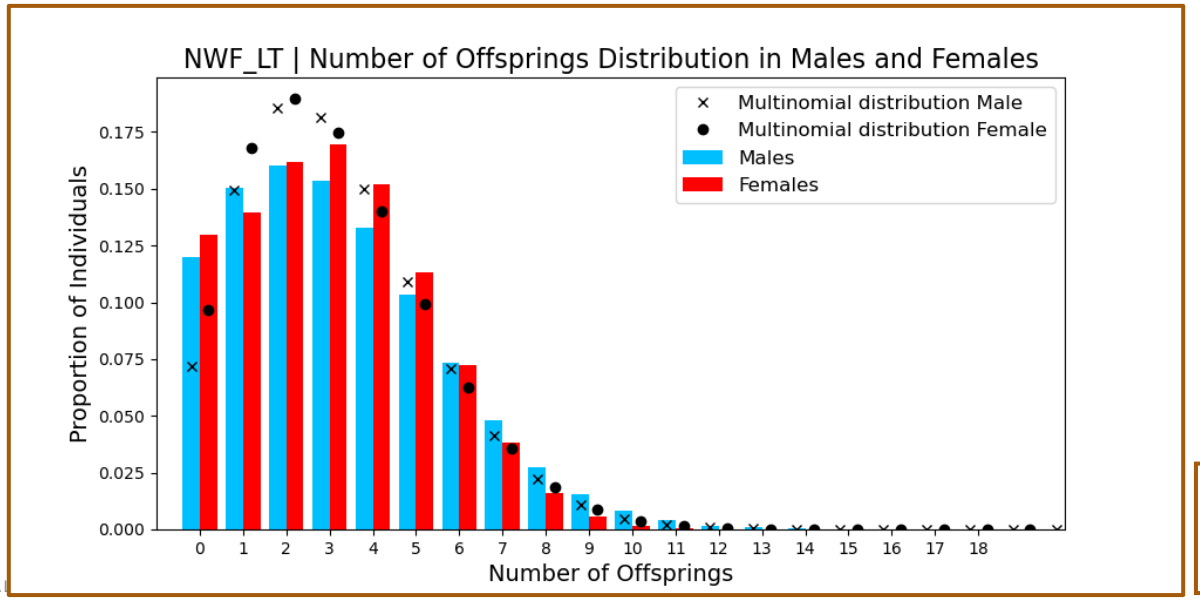
Multinomial Distribution

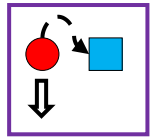
Number of Offsprings

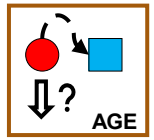












Reference Models

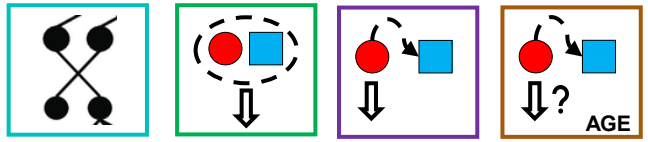
NWF models nucleotid diversity is lower than WF model one

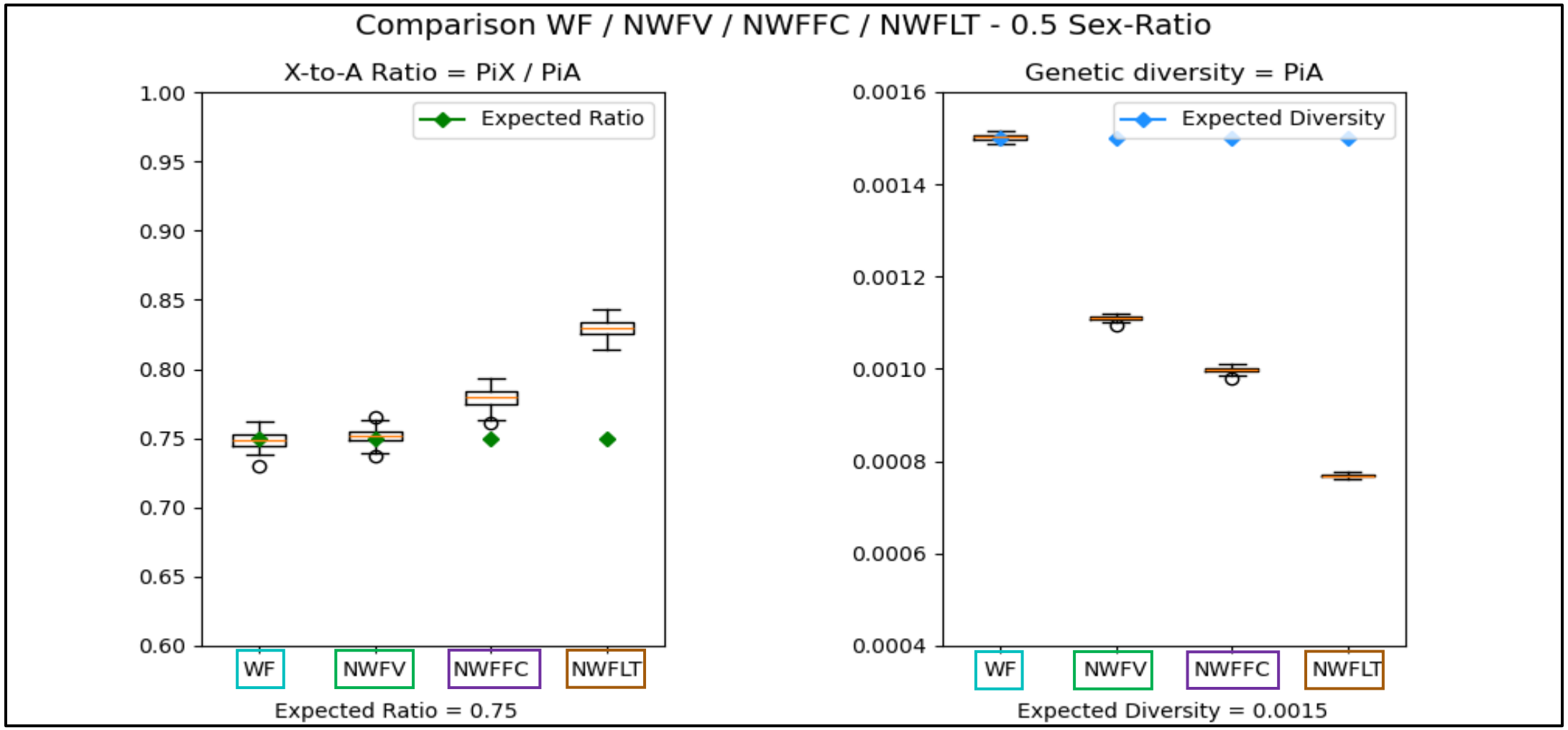
NWF_FC has a X-to-A ratio higher than expected because of random mating

NWF_LT has a X-to-A ratio higher than expected because of random mating and age structure

=> We keep NWF_LT as a reference

Reference Models





=> But Problem on NWF_LT

III. Results

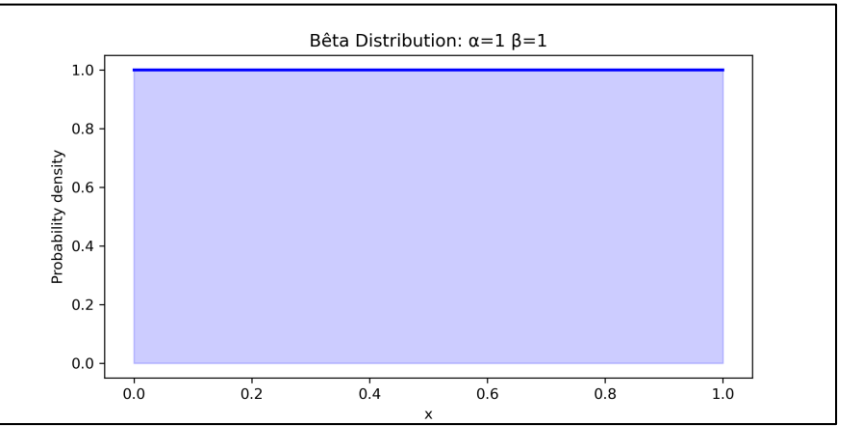
A. Males Reproductive Skew

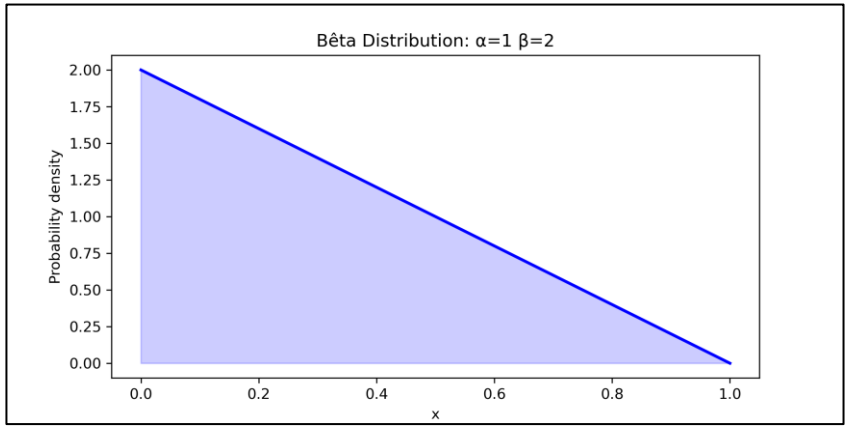
Reproductive Skew

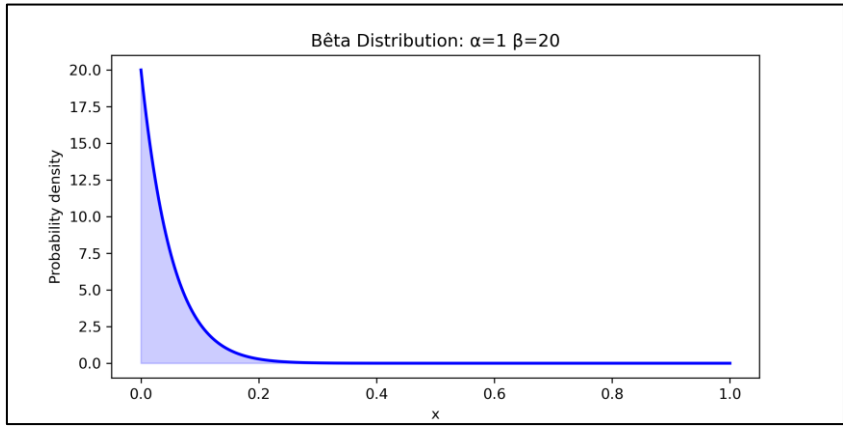
Every males gets a random Ranking value between 0 and 1

Rank determine the relative weight of the male in the reproduction following a beta distribution

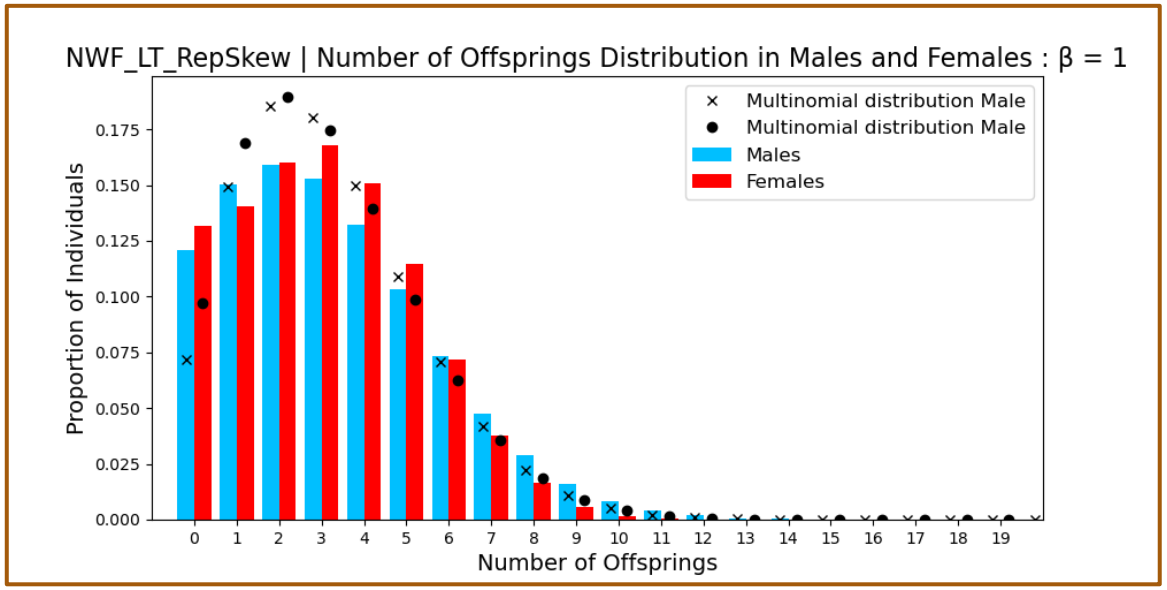
Females choose a male if their reproduction is successful

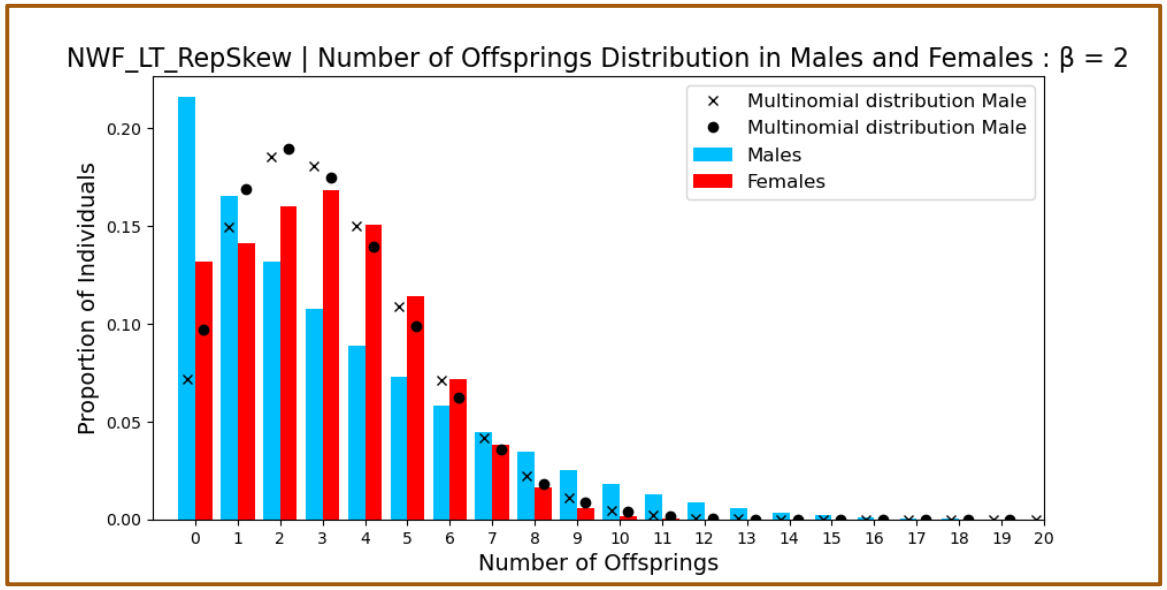


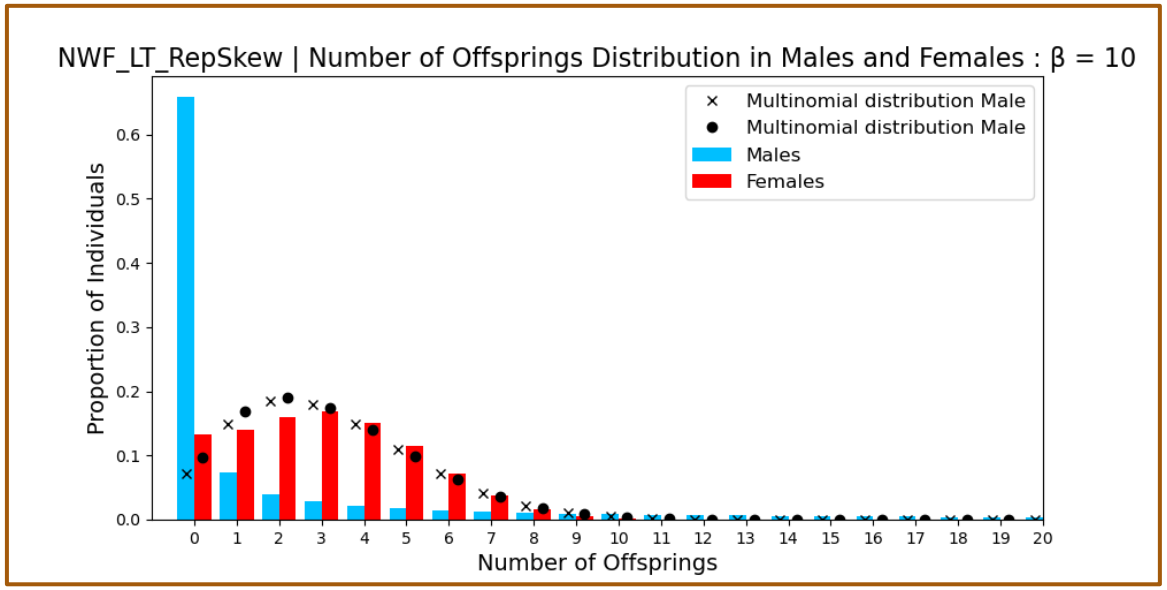


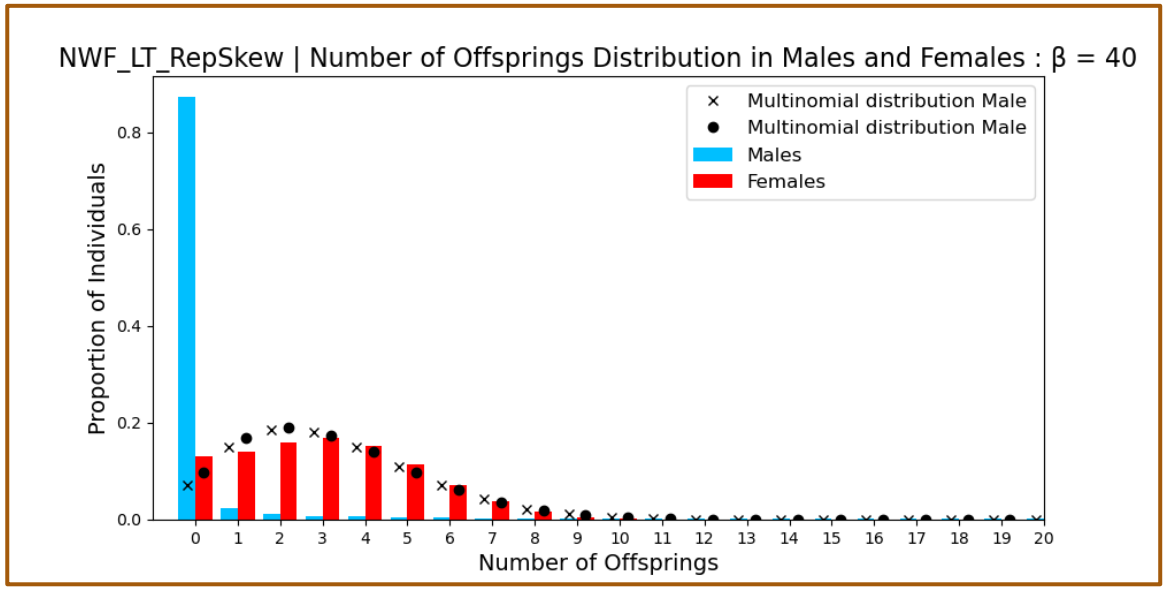


Reproductive Skew





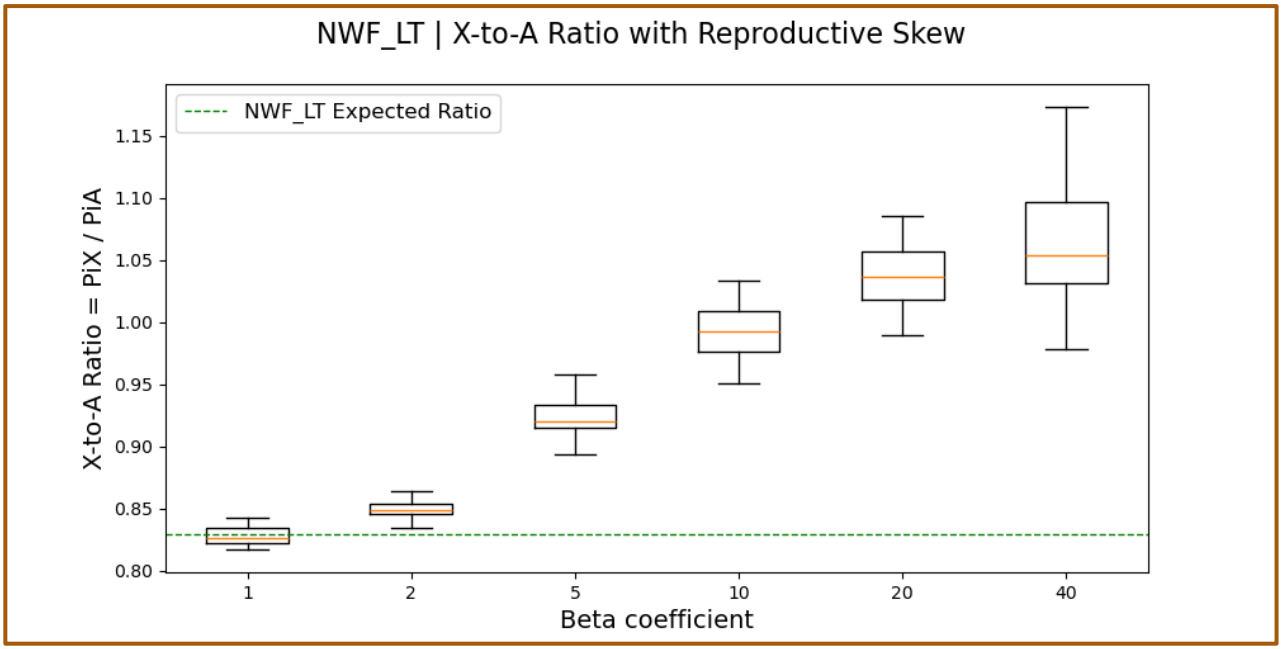


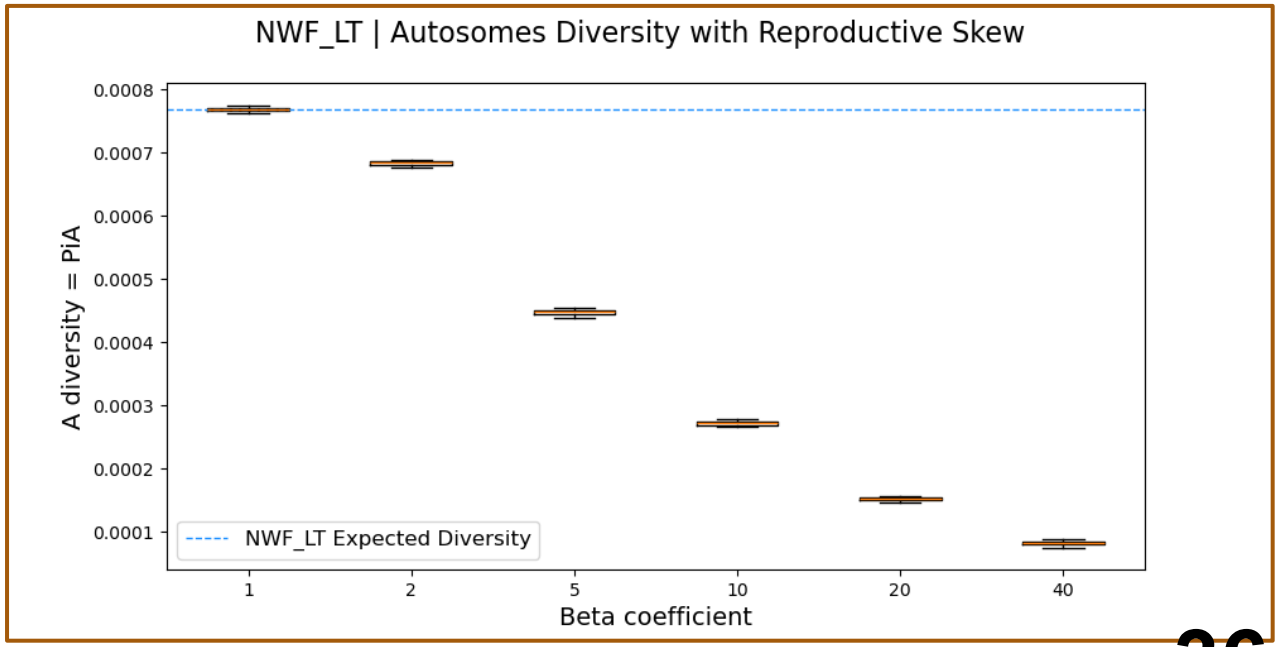


Reproductive Skew

Reproductive Skew mean of males and females for each value of Beta

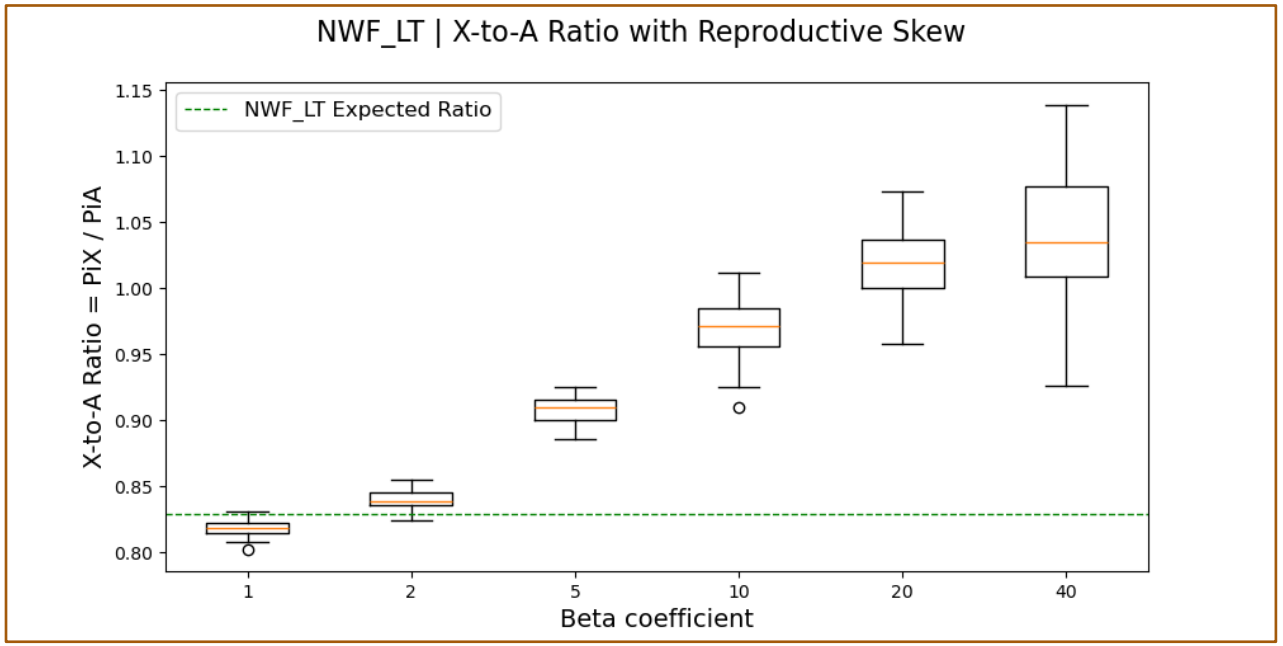
	Males	Females	Maximum	Minimum
β = 1	0.009701	-0.073462	3283.122449	-0.328291
β = 2	0.424480	-0.072683	3295.061224	-0.329395
β = 5	2.223916	-0.075689	3284.612245	-0.328614
β = 10	5.278182	-0.074994	3285.530612	-0.328832
β = 20	11.292585	-0.073673	3288.551020	-0.328719
β = 40	23.155331	-0.074022	3289.489796	-0.329085

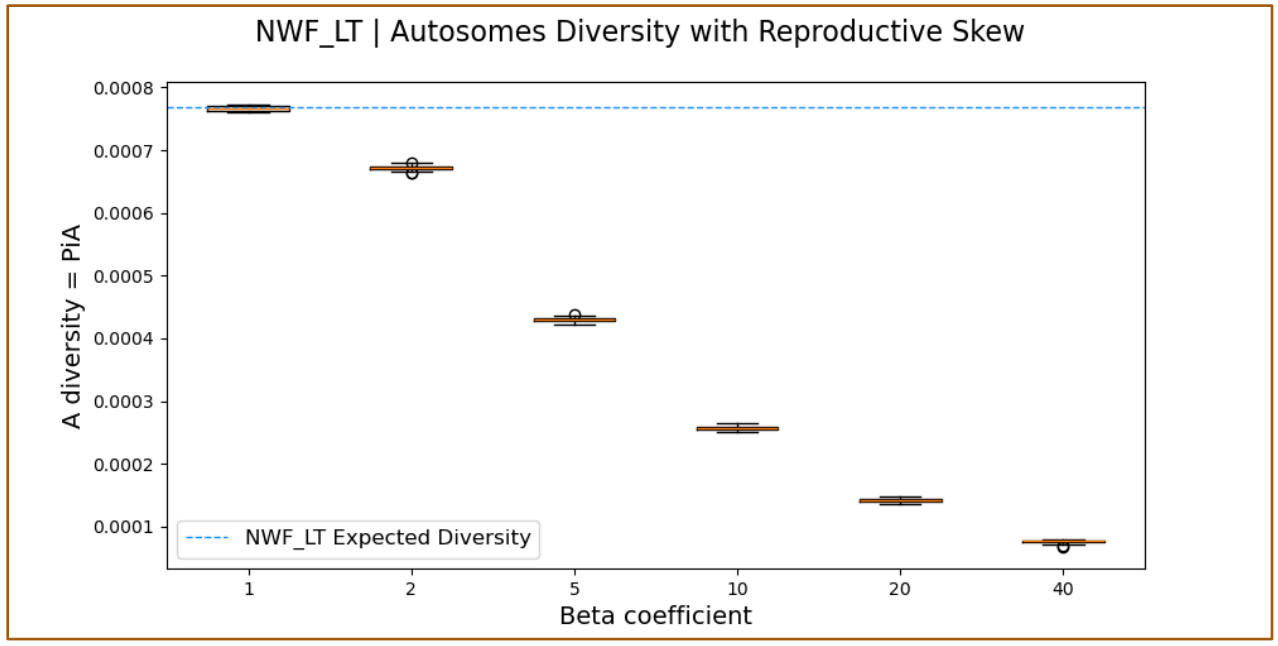




Reproductive Skew

X-to-A ratio increases when the Reproductive Skew in Males increases





In Amboseli Baboons, β might be between 2 and 5

B. Males Migration

Migration

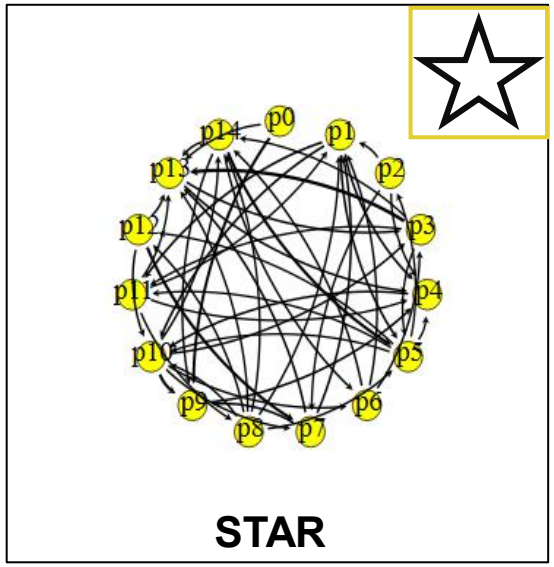
Division of the population :

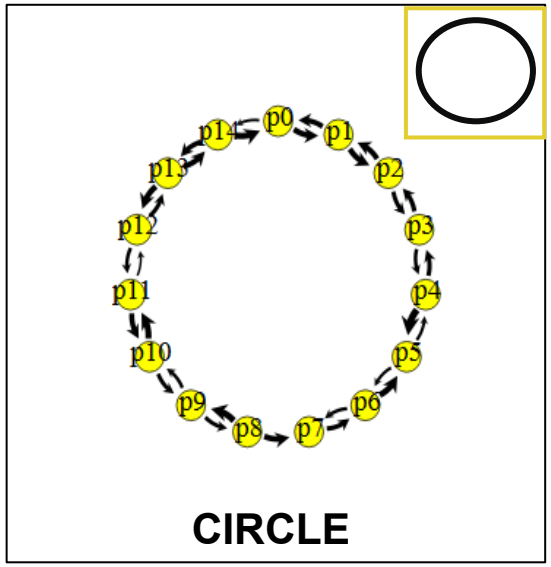
-> **15 subpopulations**

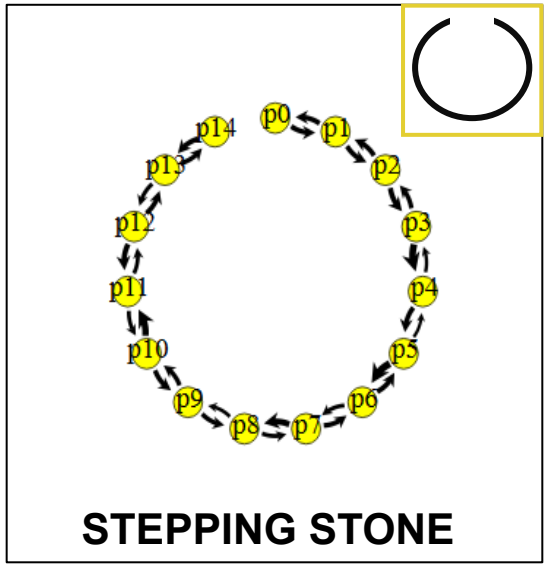
-> **50 individuals** per subpopulations

Males have a **probability to migrate every years** (when adult)

3 migrations modes :







Migration

Genetic Diversity **Estimation** :

Effective Population Size and Population Subdivision in Demographically Structured Populations, Laporte, Charlesworth 2002

For **one subpopulation**

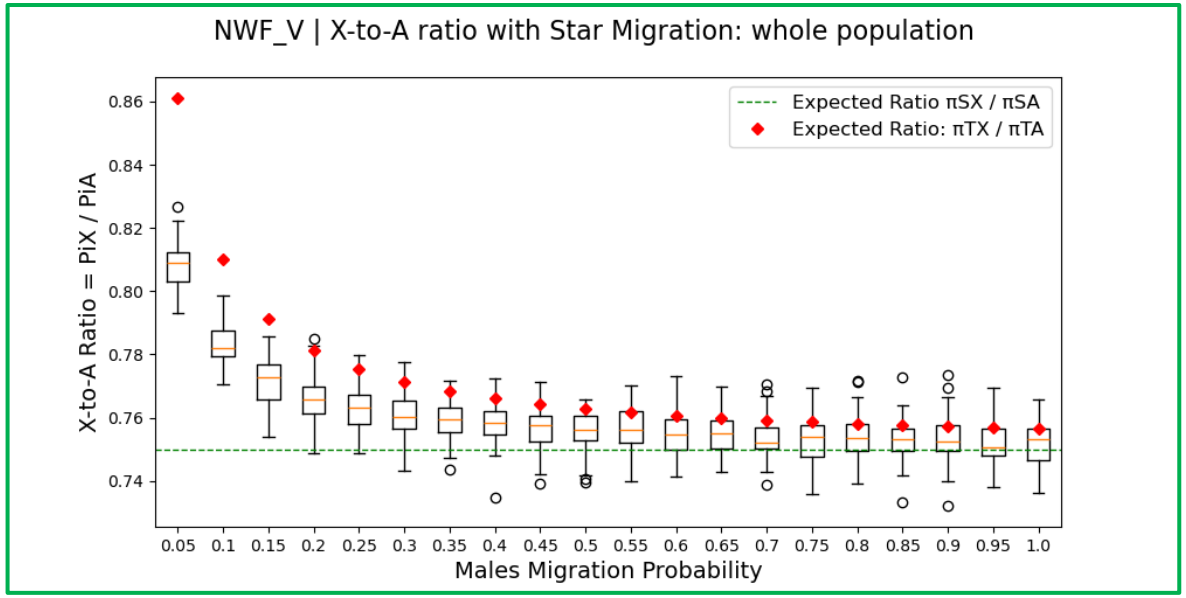
$$\boldsymbol{\pi_{SG} = 4 * n * Ne_G * \mu}$$

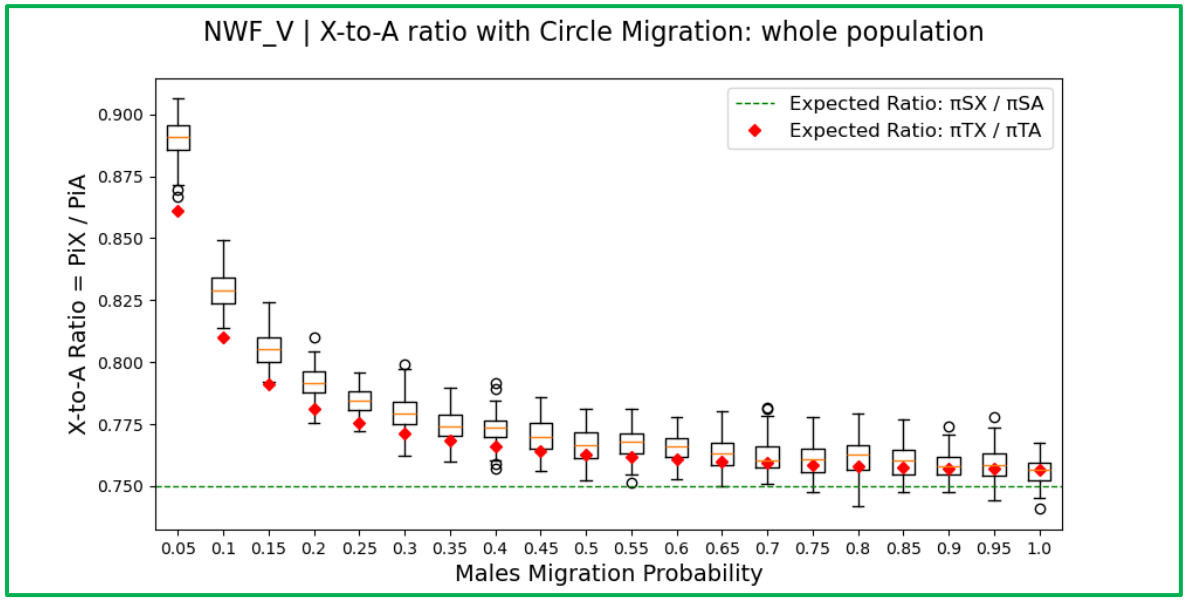
For **the whole meta-population**

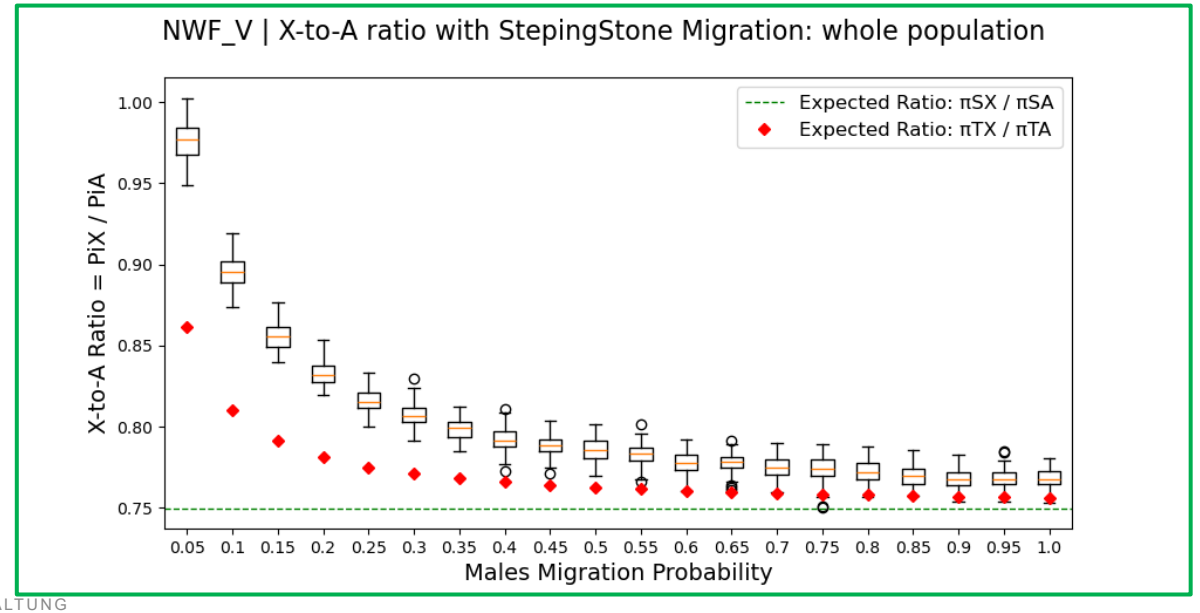
$$\boldsymbol{\pi_{TG} = \pi_{SG} * \left(1 + \frac{(n-1)^2}{n^2} \frac{1}{4 * m_g * Ne_G}\right)}$$

$$m_X = \frac{1}{3}(m_{Male} + 2 * m_{Female}) \qquad m_A = \frac{1}{2}(m_{Male} + m_{Female})$$

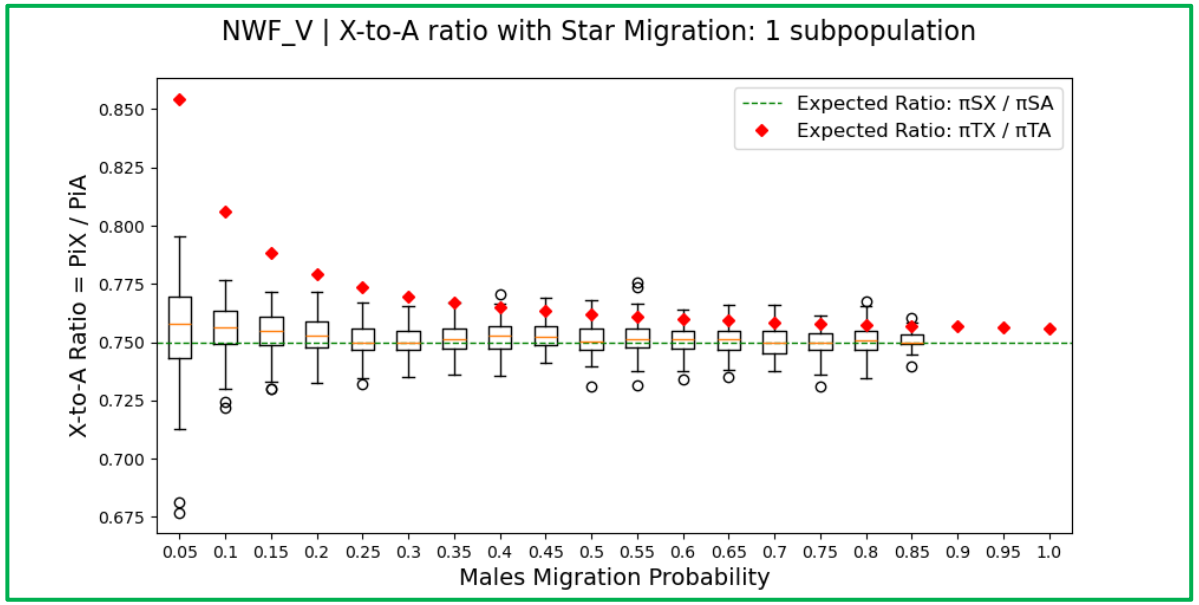
Migration: NWF_V whole Population

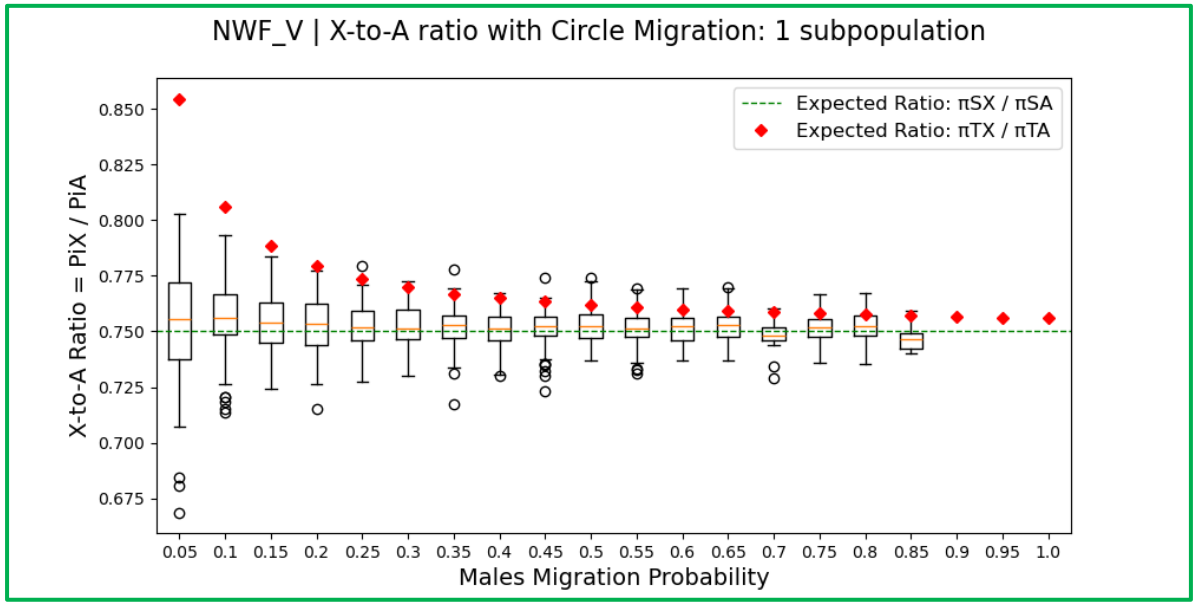


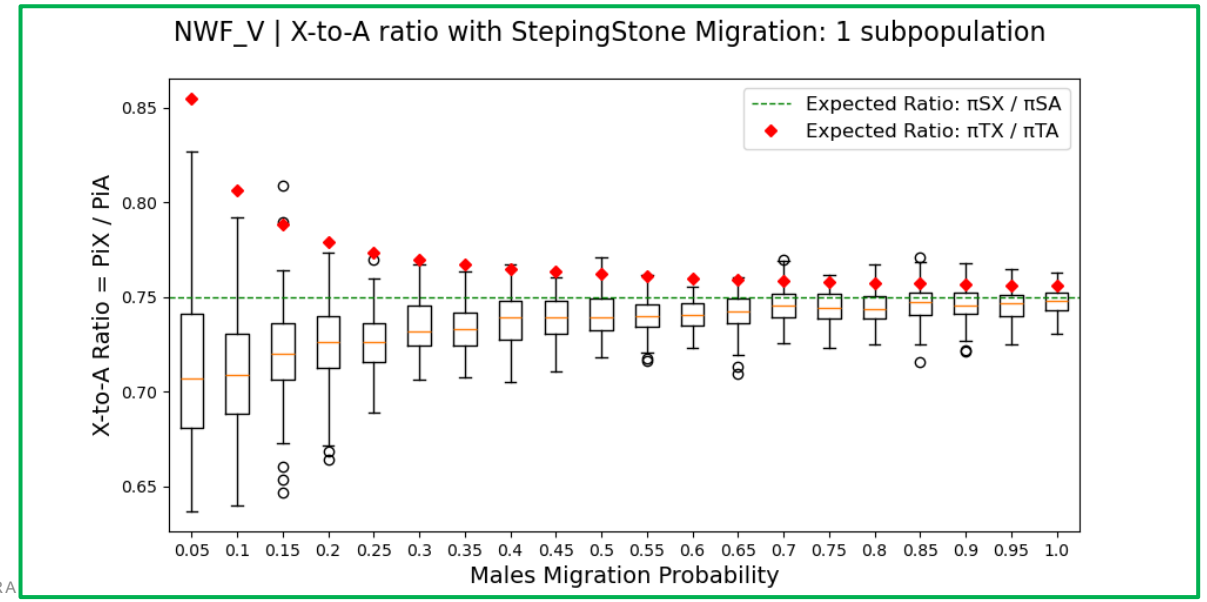




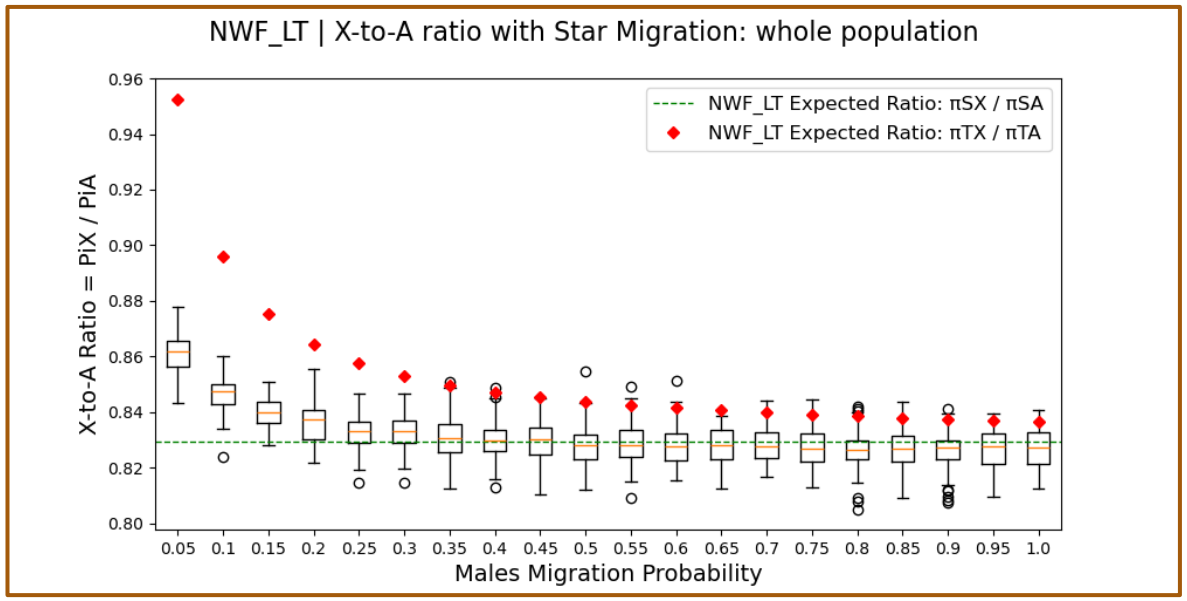
Migration: NWF_V one SubPopulation

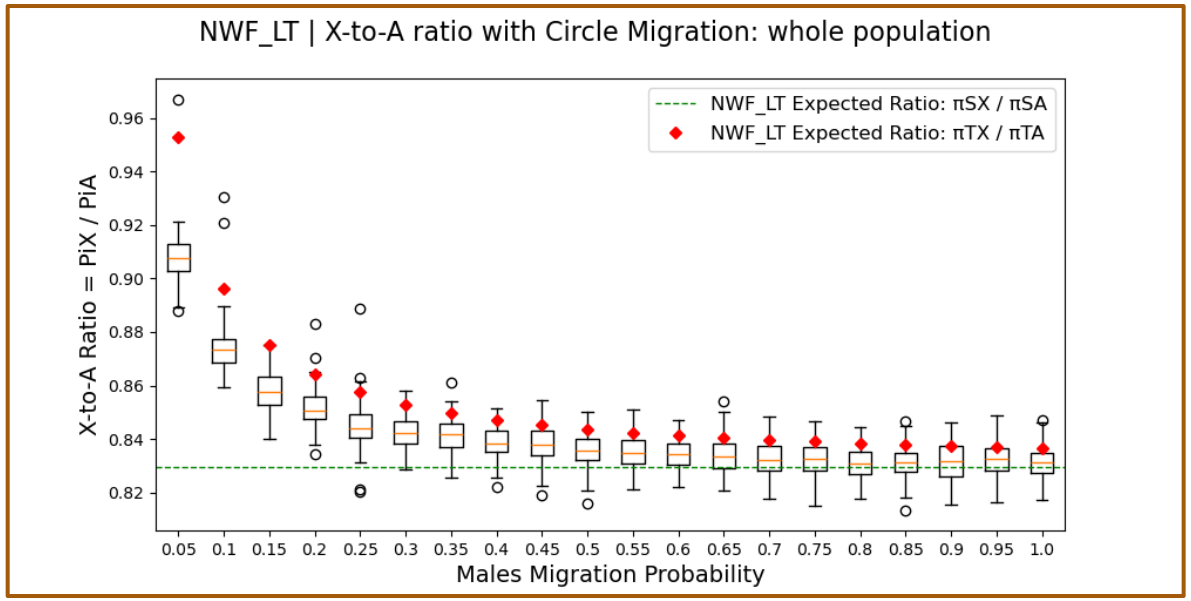


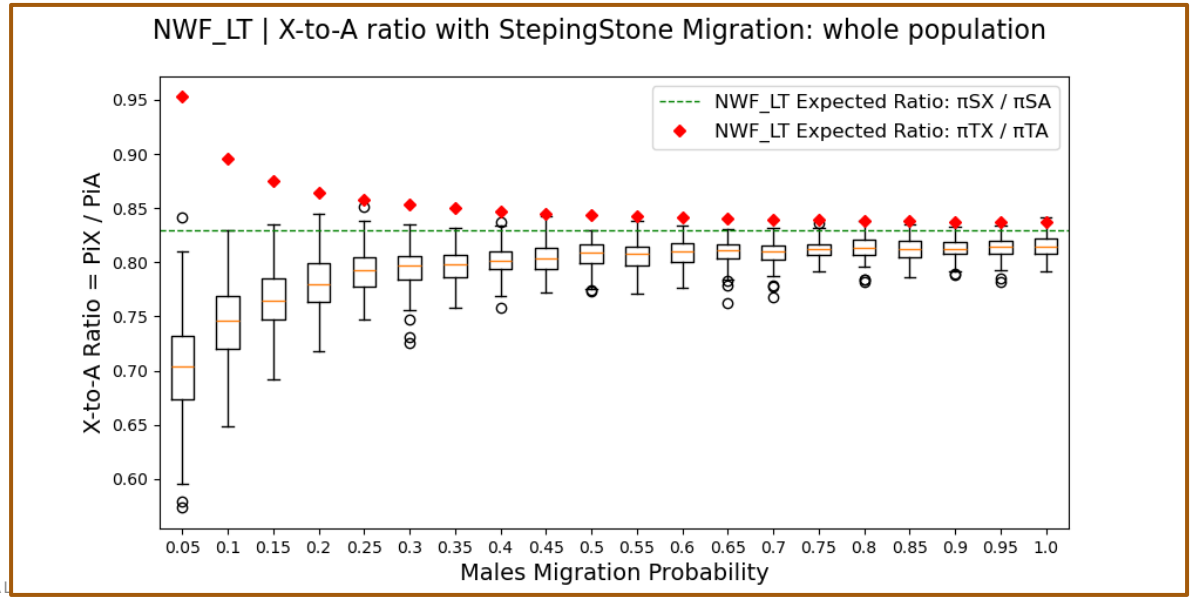




Migration: NWF_LT whole Population





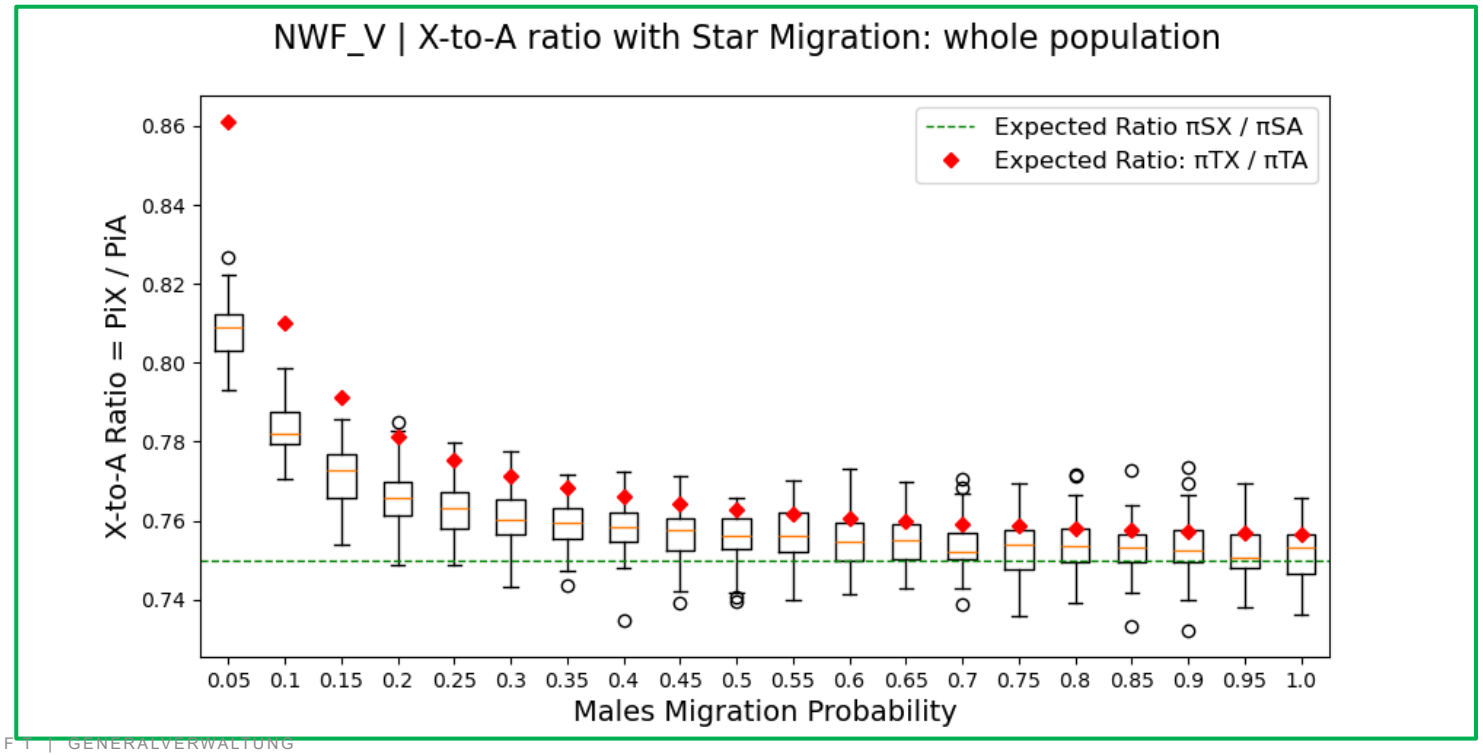


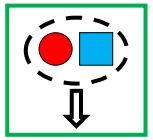
Migration

X-to-A ratio decreases when the migration probability increases

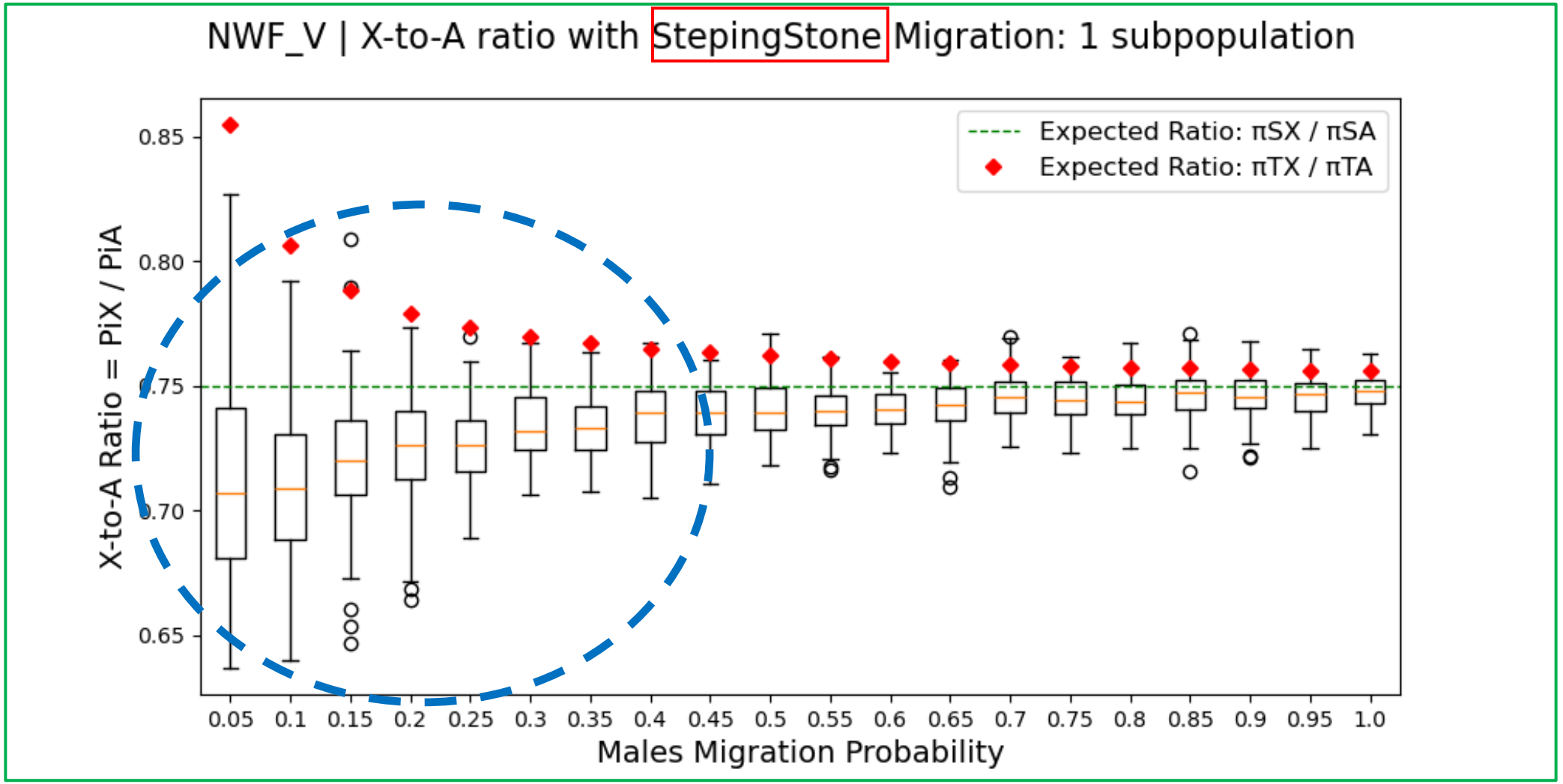
In Amboseli, every males migrate

Males only Migration does not strongly change the X-to-A ratio





Migration: NWF_V One SubPopulation



=> The X-to-A ratio decreases in diverged populations

C. Hybridization Without Selection

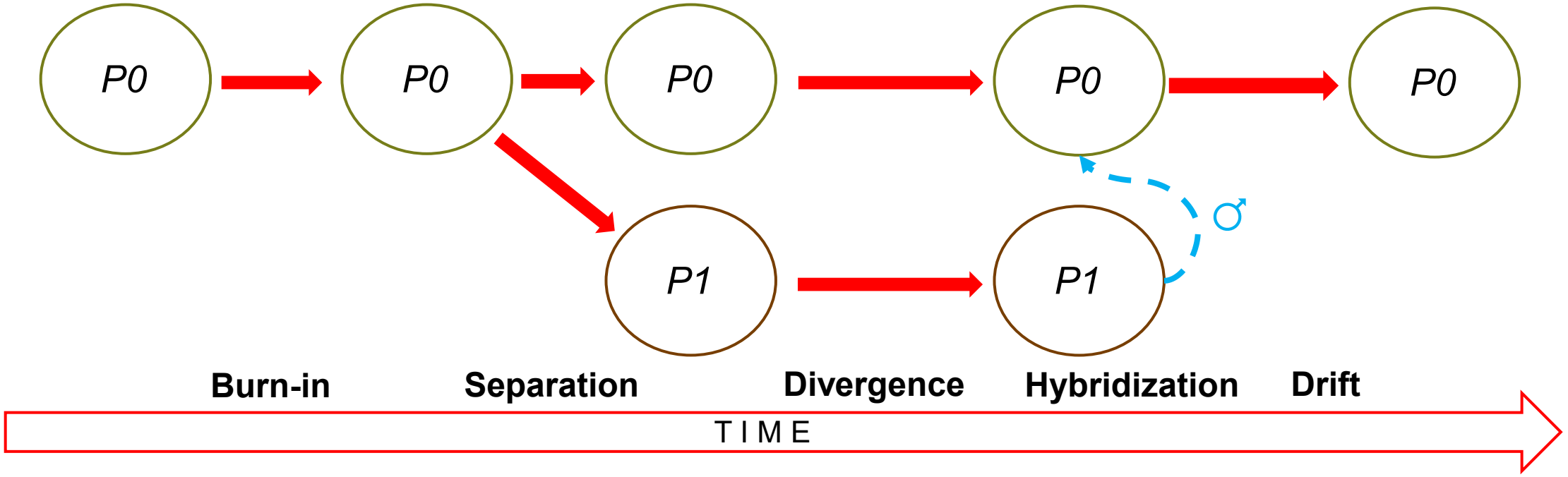
Hybridization

Simulations in 3 Periods:

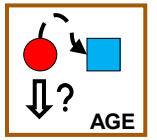
1) **One population** (*P0*) of 750 individuals for 60000 Ticks

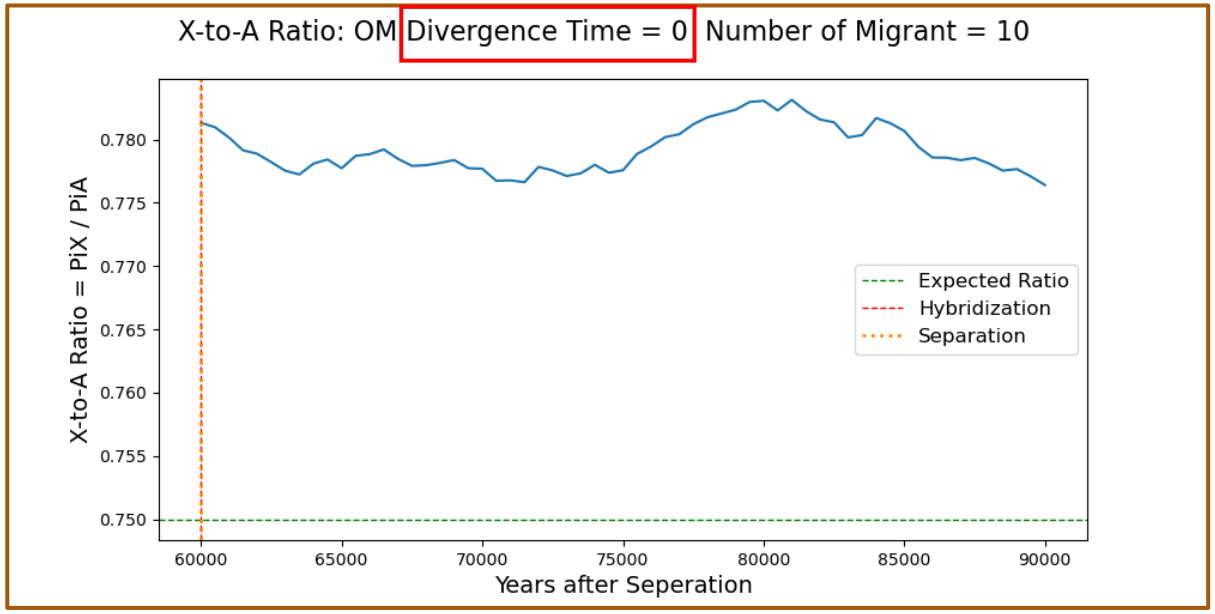
2) **Division in two isolated populations** (*P0* and *P1*) for a tunable time

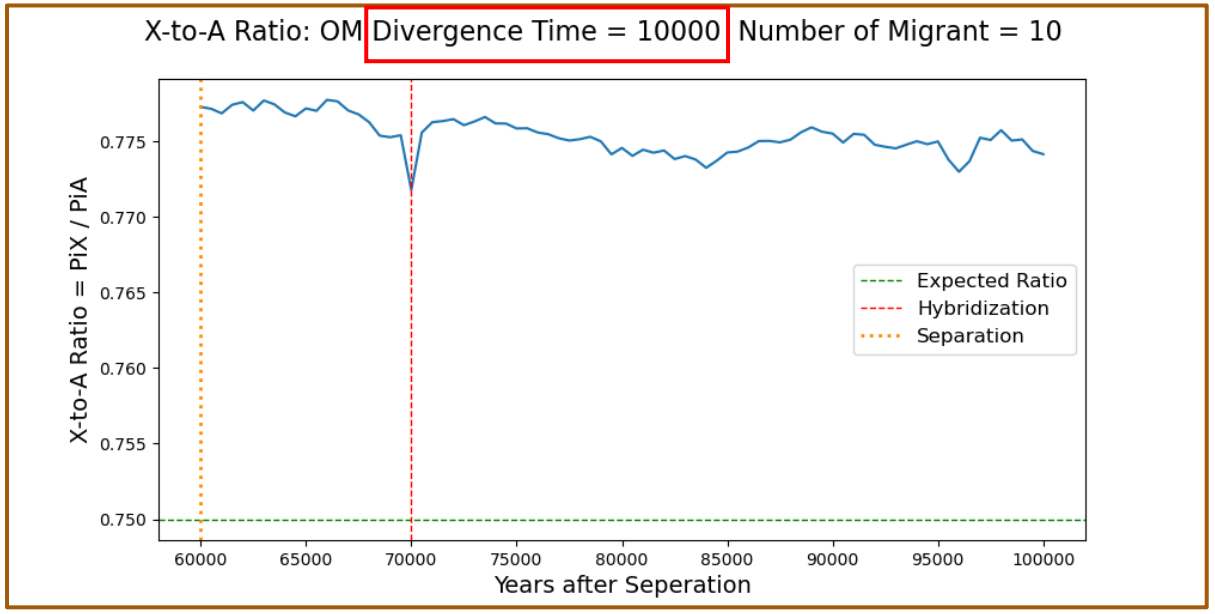
3) **1 Migration** of males from *P1* to *P0* and **Drift** of *P0* for 30000Ticks

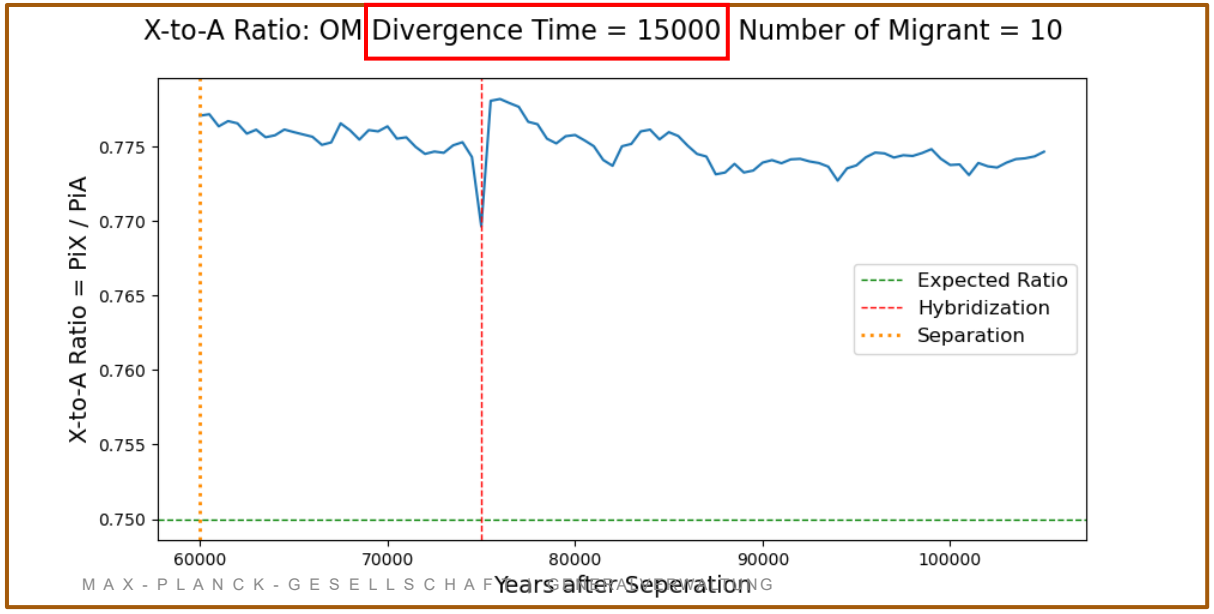


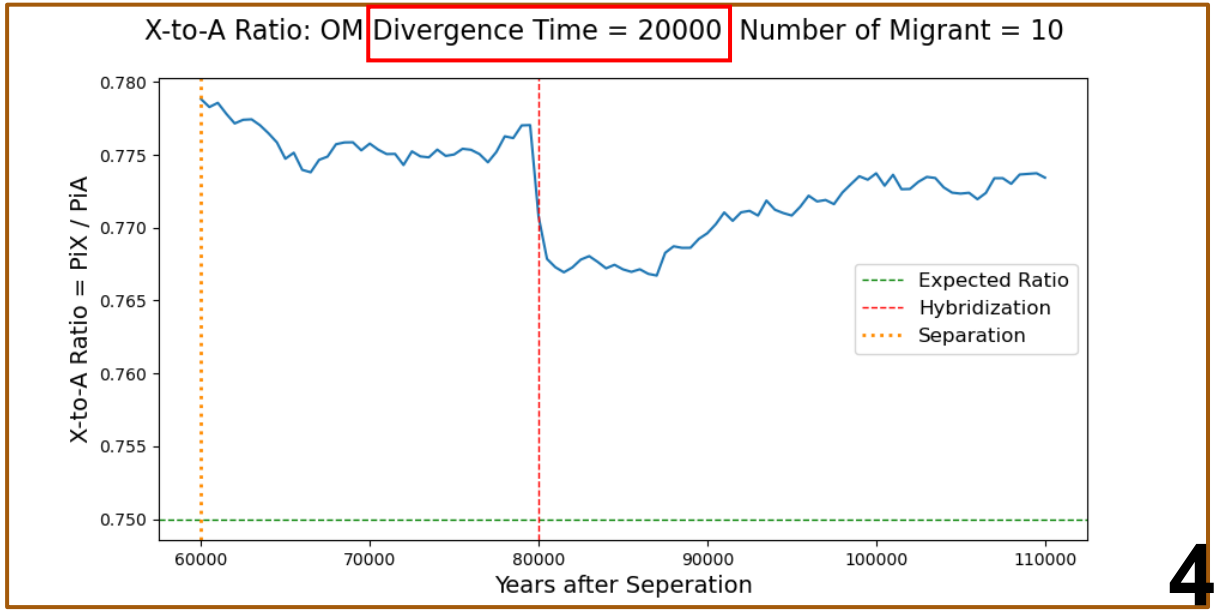
Hybridization 10 Migrants



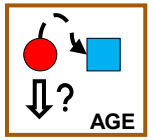


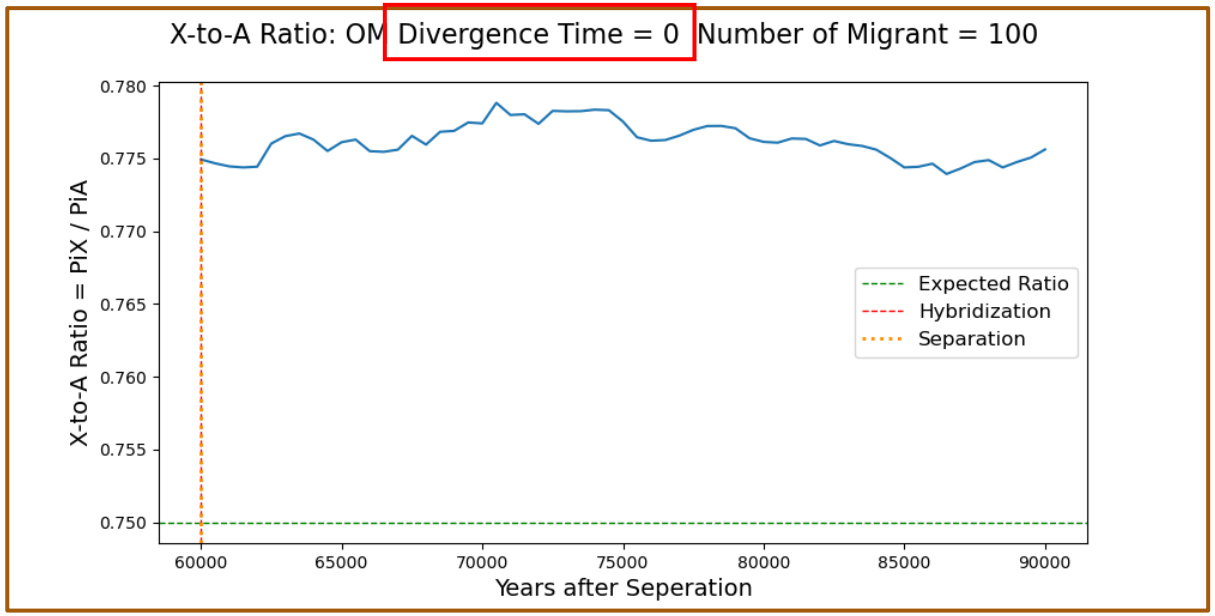


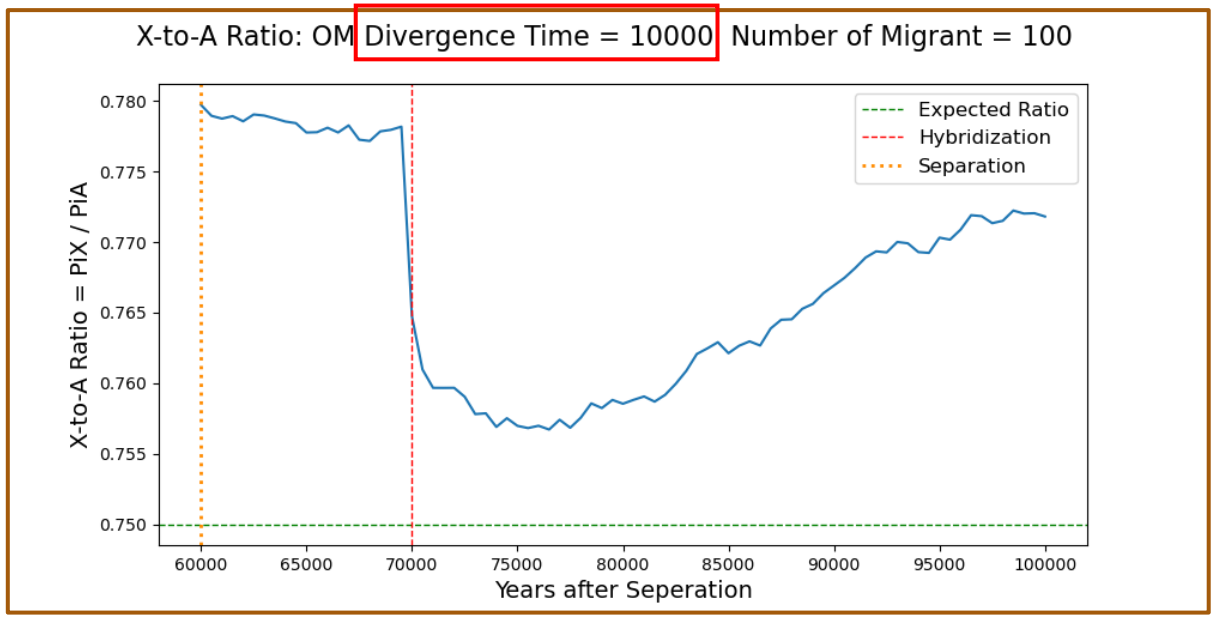


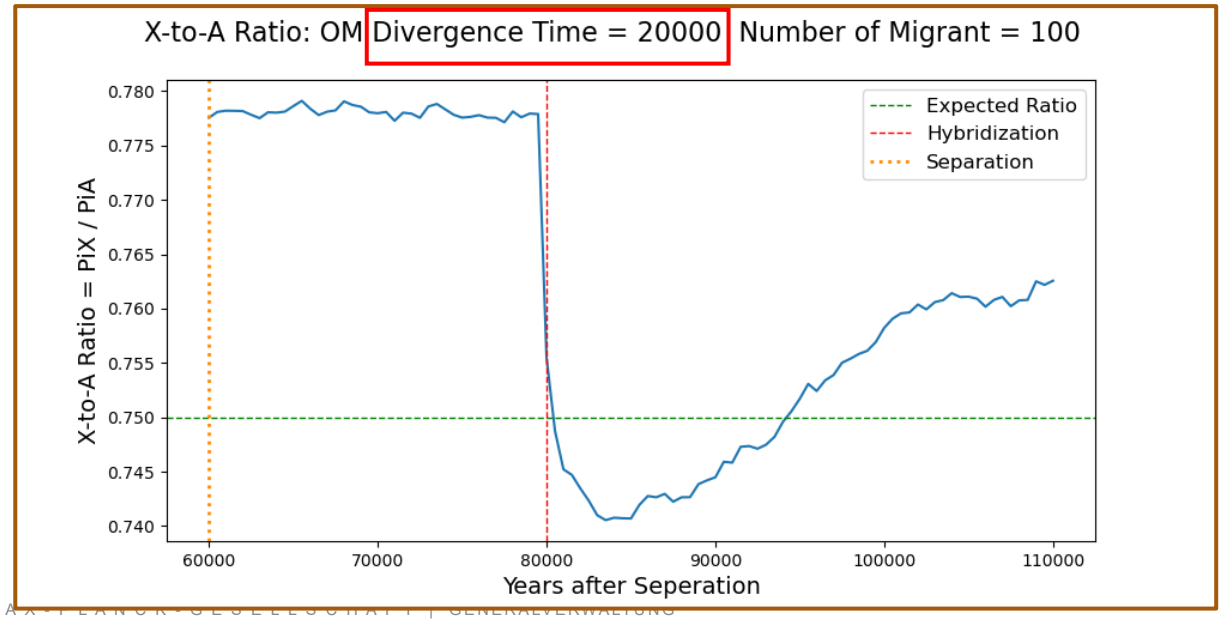


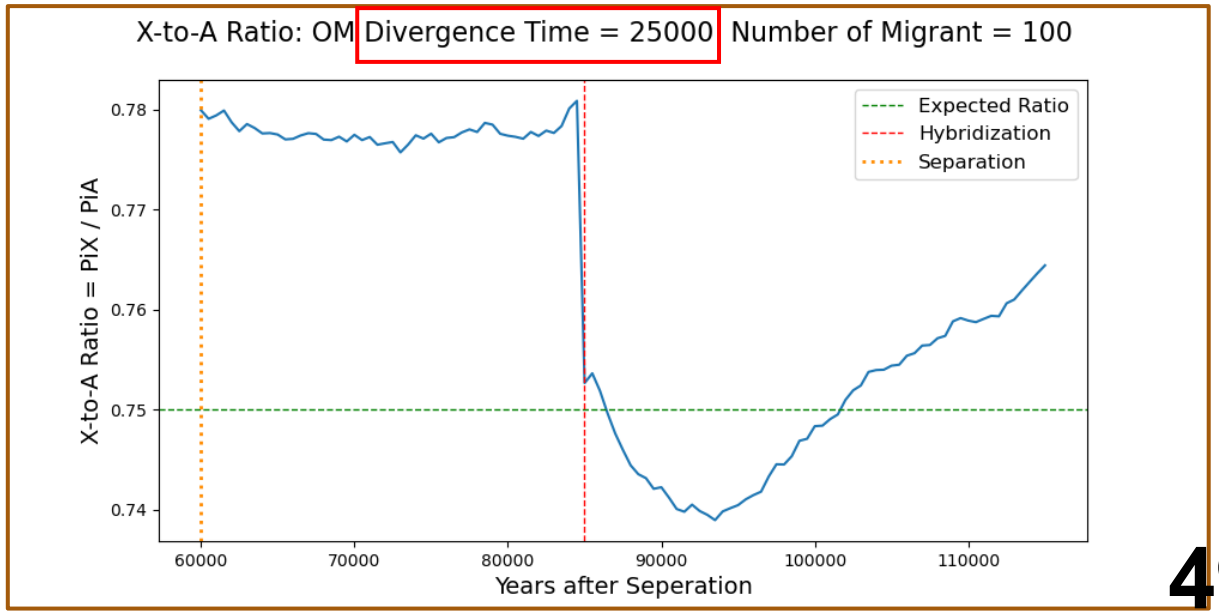
Hybridization 100 Migrants











Hybridization

Hybridization with male migration decreases the X-to-A ratio

The more diverged populations are, the stronger the effect is

Hybridization

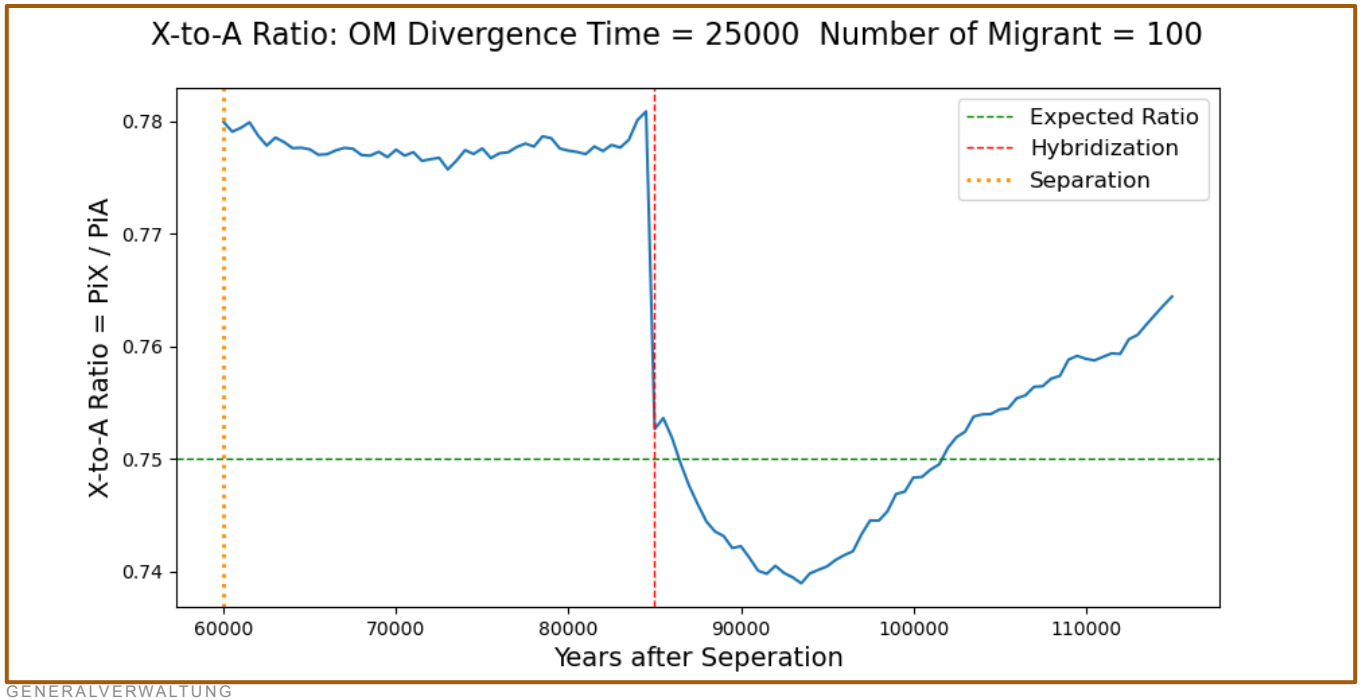
Selection against admixture and gene regulatory divergence in a long-term primate field study, Vilgalys & al (2022)

Genetic structure in a dynamic baboon hybrid zone corroborates behavioural observations in a hybrid population, Charpentier & al (2012)

In Amboseli:

- **Hybridization** occurred **several times** since 1980, with **low number** of migrants

- The **time of divergence** is around **1,5 million years**



D. Selection

Background Selection

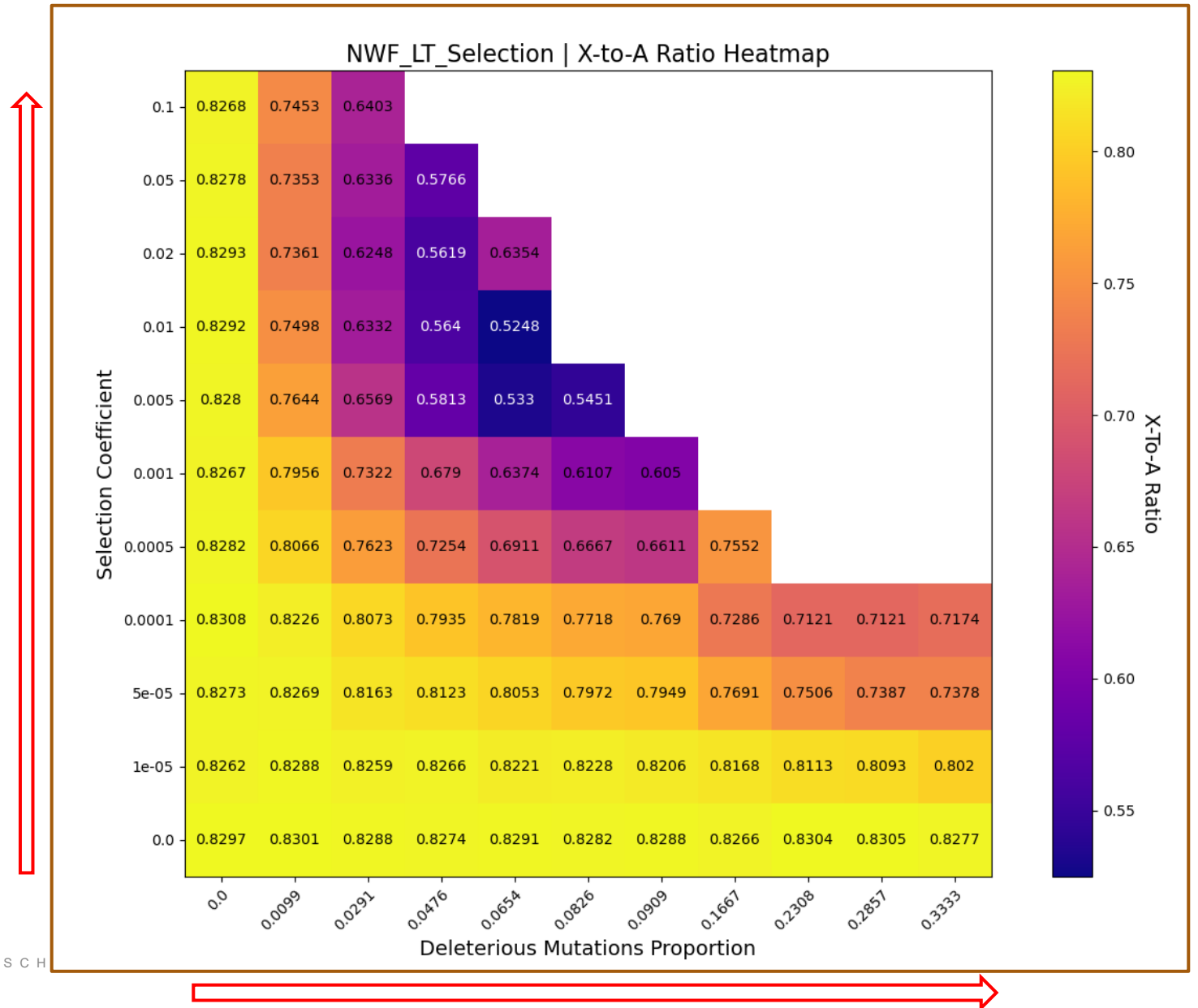
Background Selection = loss of diversity due to negative selection against deleterious mutations

Deleterious mutations only on X :

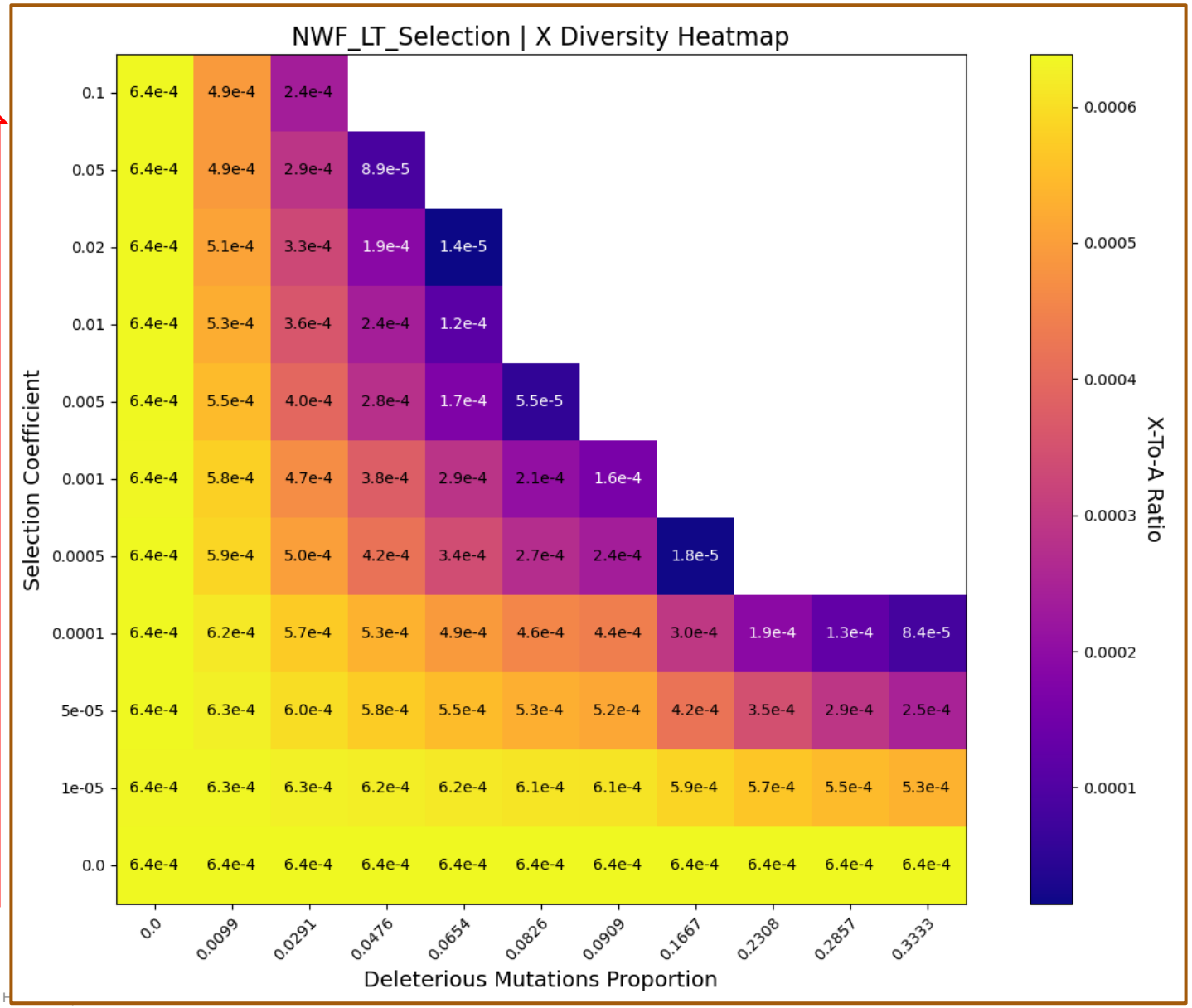
- **Selective Coefficient** following a gamma distribution (γ = 1)
- **Proportion of Deleterious Mutations**

Mutations Rate : **5e-7 mut.nuceotide^{-1}.tick^{-1}**

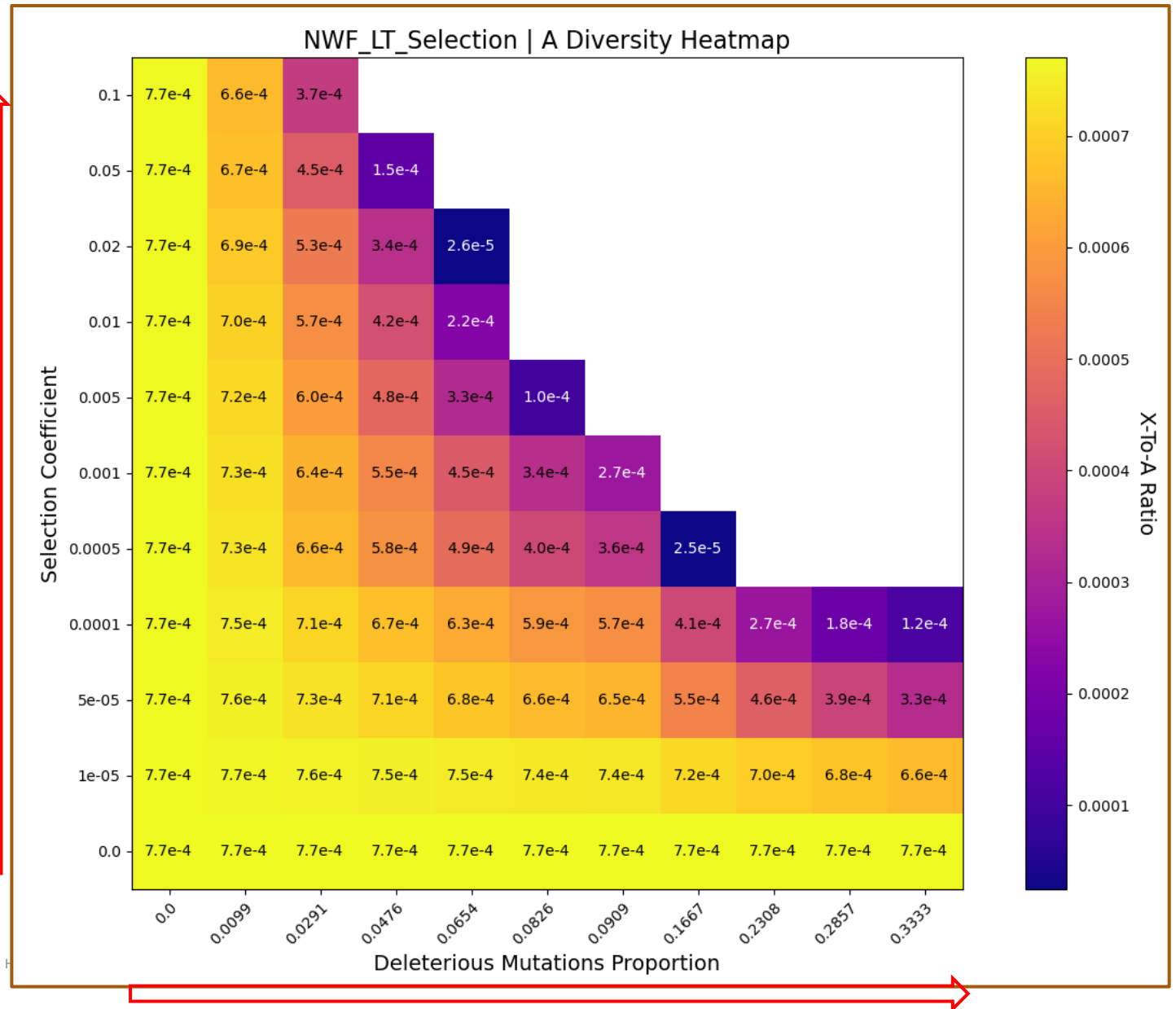
Selection : X-to-A Ratio



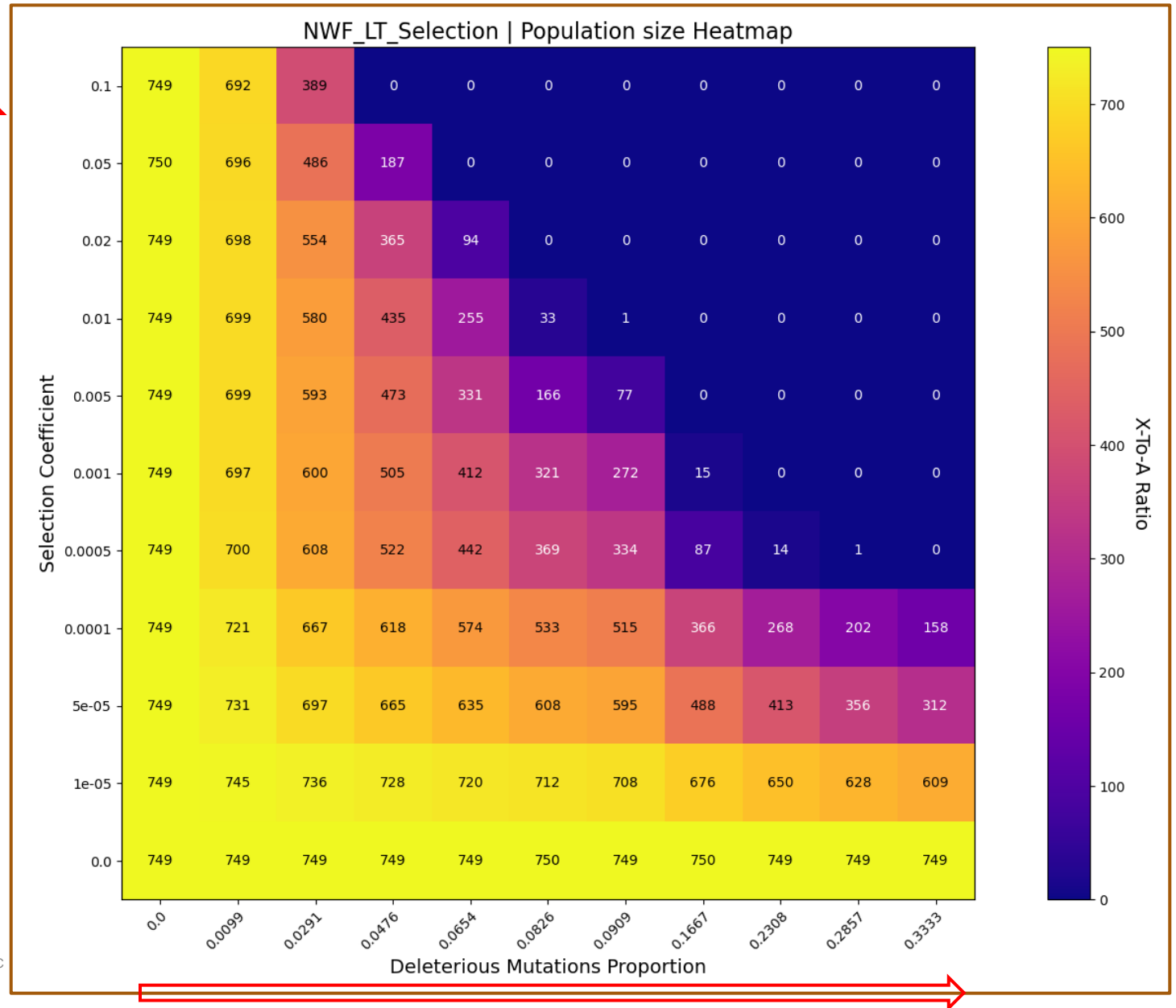
Selection : X Diversity



Selection : A Diversity



Selection : Population Size



Selection

The more deleterious mutations are, the more the X-to-A ratio is decreased

The higher the deleterious mutations proportion is, the more the X-to-A ratio is decreased

Selection decreases also the population size

IV. Conclusion

Forces and Diversity

2 Sex-biased processes affect the X-to-A ratio**:**

- **Reproductive Skew in males** increases it ↗
- **Hybridization** decreases it ↘

Selection on X decreases the ratio ↘

Present Work Limits

- Population Rescaling
- Burn-in Period changes with different processes
- Missing some forces on the X-to-A ratio
- Lack of Data for field study–informed Modeling

Next Steps

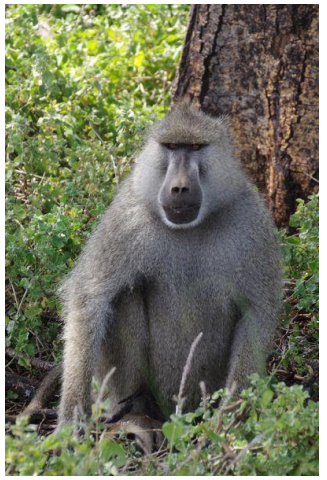
$\Rightarrow$ **Keep Using SLiM**

Many forces in same simulations :

- Reproductive skew Vs Selection
- Hybridization Vs Selection

New assumptions to simulate forces

Thank You !!!



The PrimEvo Department for the welcoming !

My Internship advisors :

Iker Rivas-Gonzalez

Jenny Tung

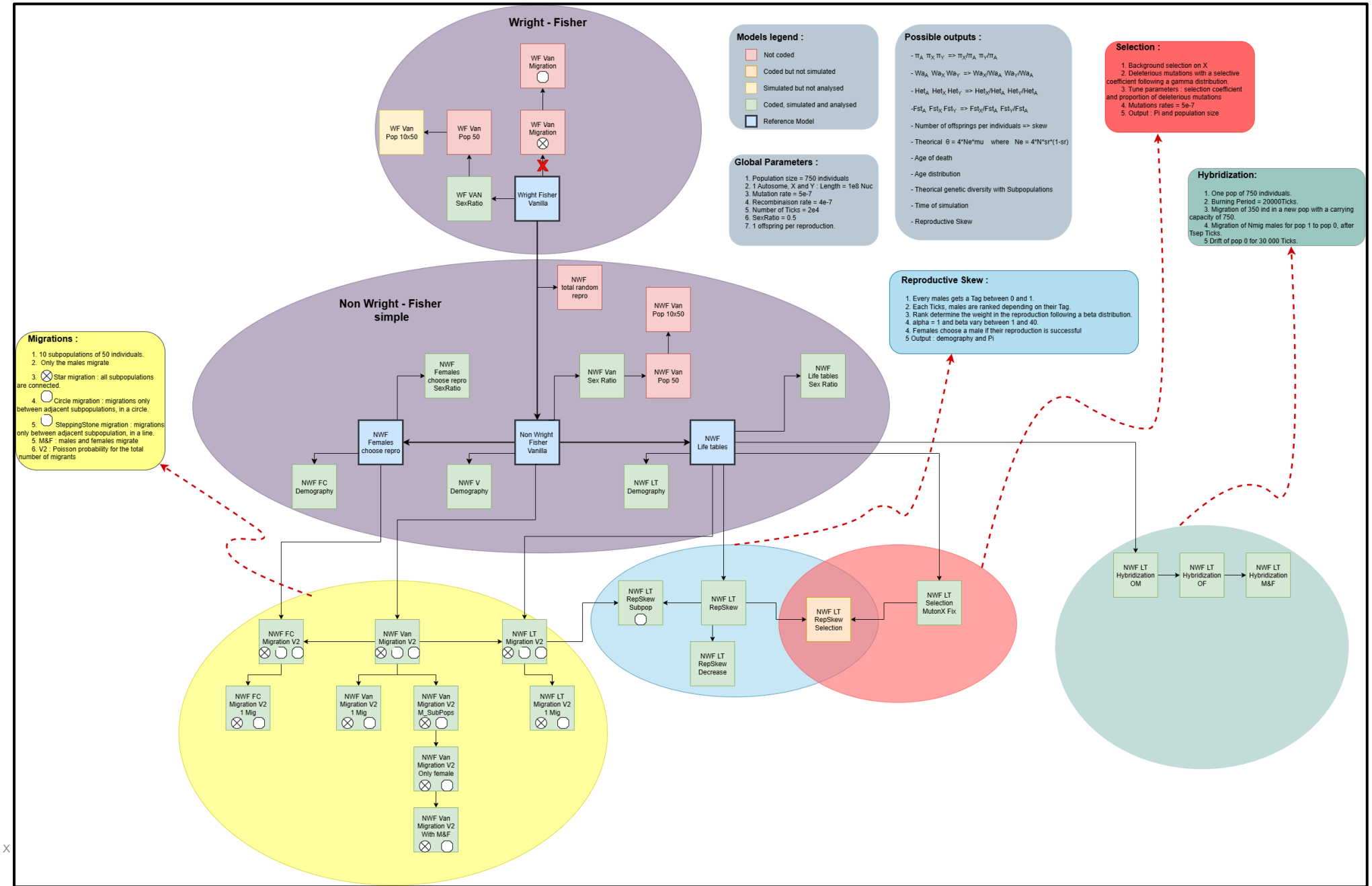
Pierre Gerard

MAX PLANCK INSTITUTE
FOR EVOLUTIONARY ANTHROPOLOGY

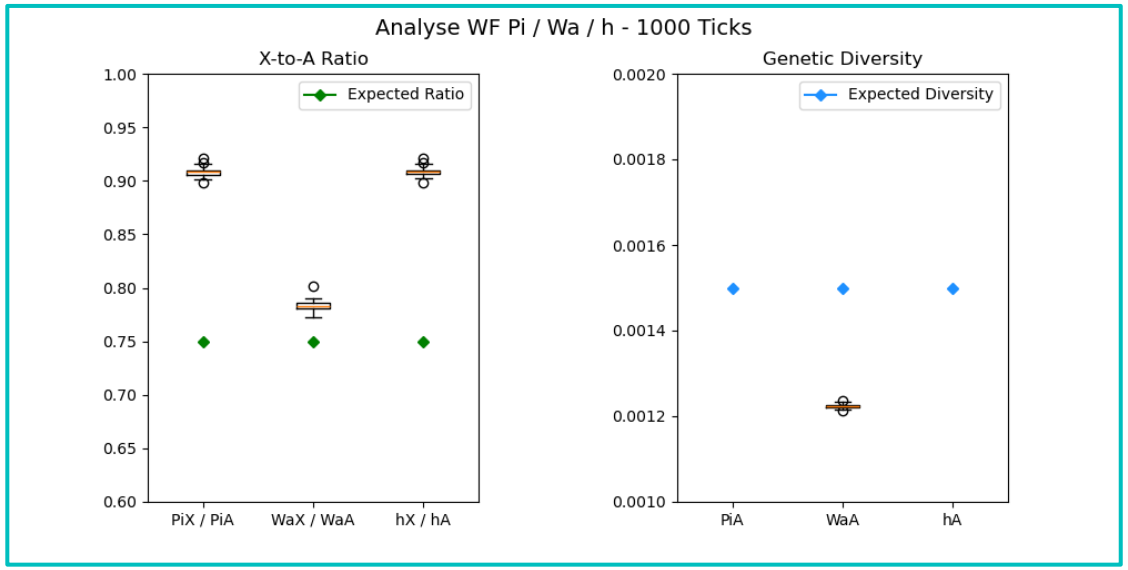
AgroParisTech

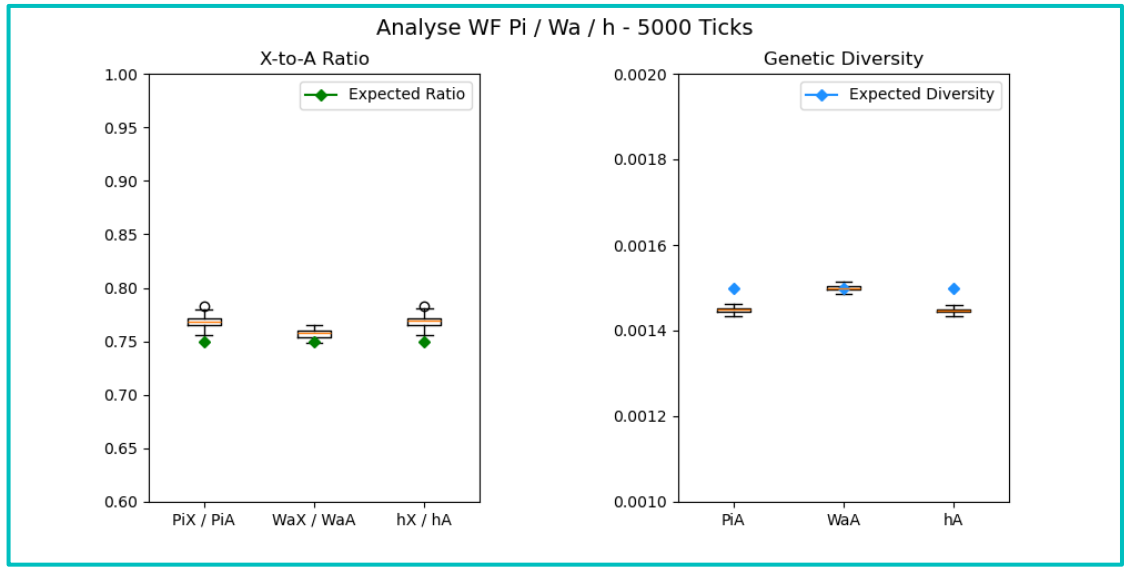
V. Annexes

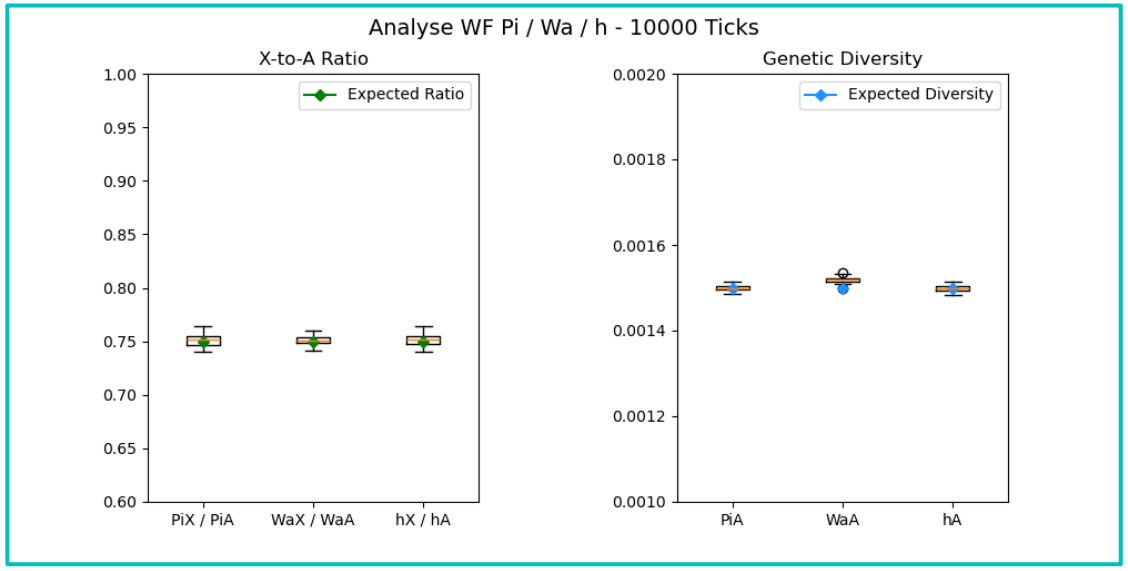
Mind Map Simulations

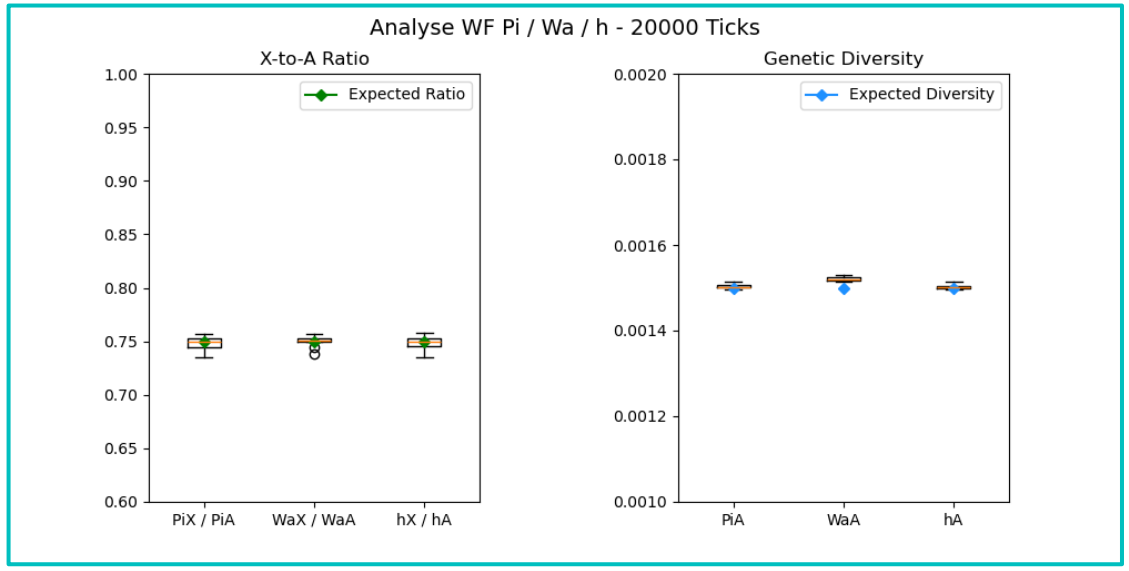


WF : Number of Ticks

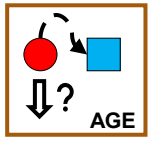








Life Tables



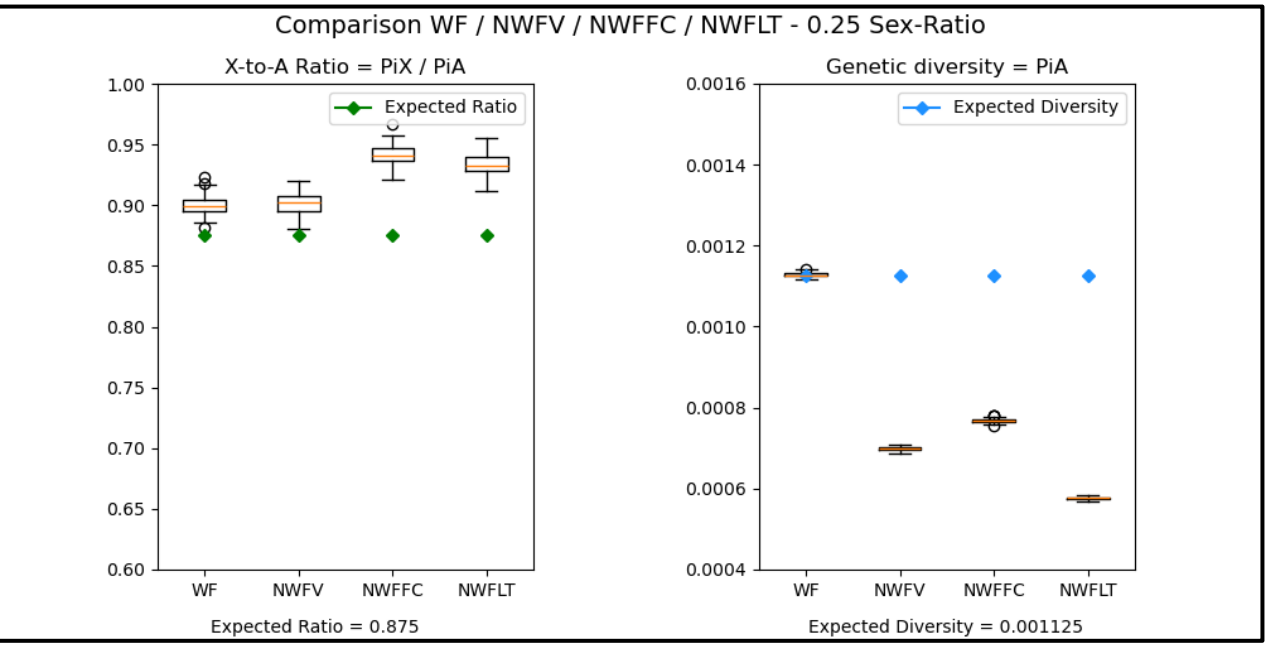
Age	Female_Mortality	Male_Mortality	Female_fecundity
0.0	0.215909091	0.215809285	0.0
1.0	0.092391304	0.096	0.0
2.0	0.045908184	0.076106195	0.0
3.0	0.054393305	0.057471264	0.0
4.0	0.037610619	0.042682927	0.005
5.0	0.03908046	0.050955414	0.211
6.0	0.04784689	0.049217002	0.264
7.0	0.037688442	0.058823529	0.272
8.0	0.041775457	0.06	0.279
9.0	0.046321526	0.02393617	0.281
10.0	0.034285714	0.068119891	0.269
11.0	0.065088757	0.067251462	0.276
12.0	0.060126582	0.112852665	0.29
13.0	0.087542088	0.091872792	0.291
14.0	0.081180812	0.112840467	0.285
15.0	0.088353414	0.140350877	0.274
16.0	0.083700441	0.137755102	0.263
17.0	0.125	0.165680473	0.271
18.0	0.093406593	0.219858156	0.271
19.0	0.163636364	0.254545455	0.236
20.0	0.115942029	0.329268293	0.233
21.0	0.147540984	0.345454545	0.259
22.0	0.240384615	0.416666667	0.047
23.0	0.164556962	0.476190476	0.108
24.0	0.333333333	1.0	0.0
25.0	0.363636364	1.0	0.0
26.0	0.428571429	1.0	0.0
27.0	1.0	1.0	0.0

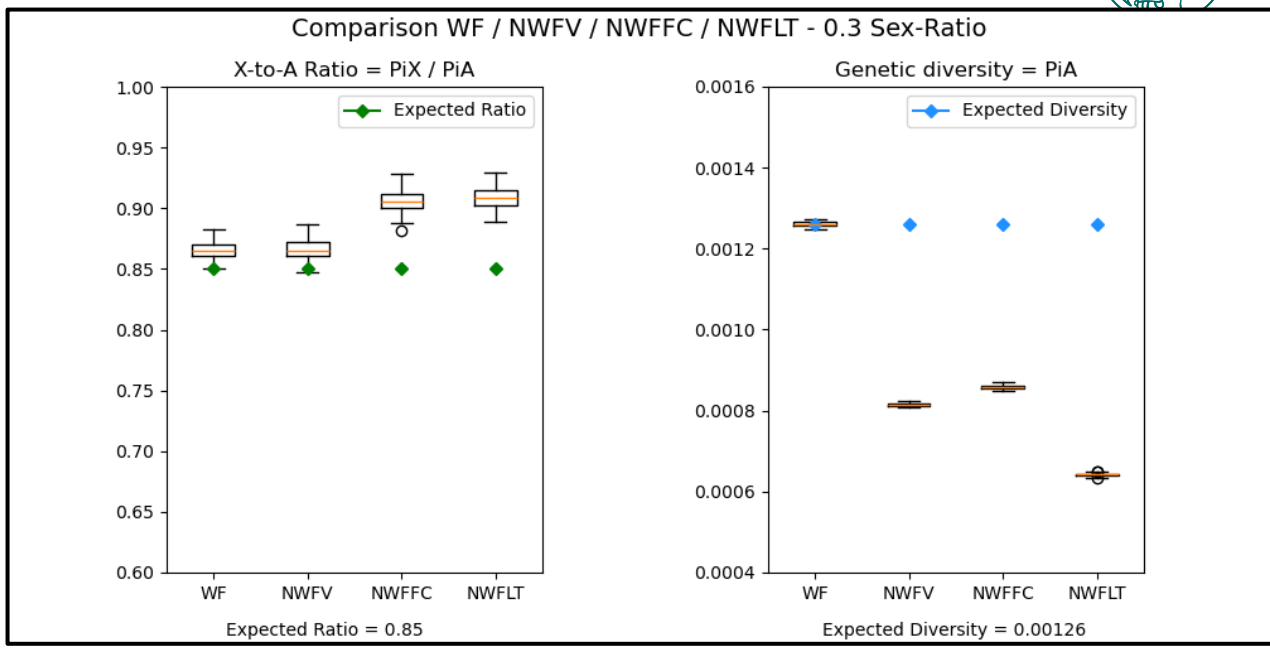
NWF_LT Median Ratio: 0.8296

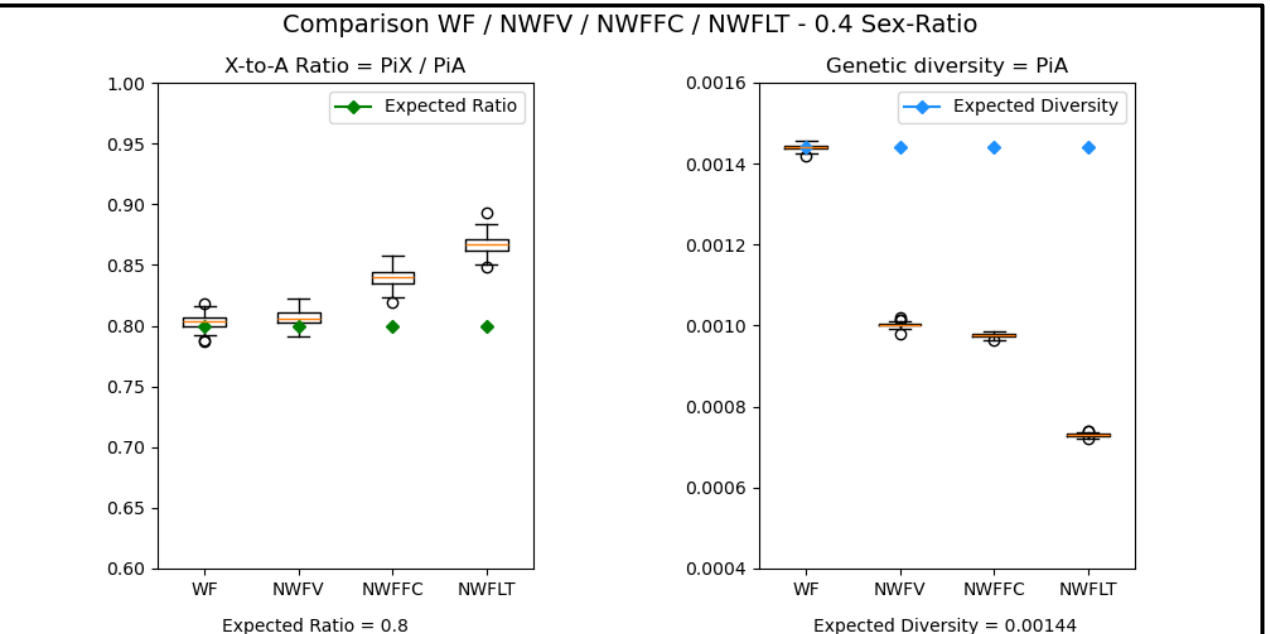
Median Pi Autosome: 0.0007692
Median Pi X: 0.0006381

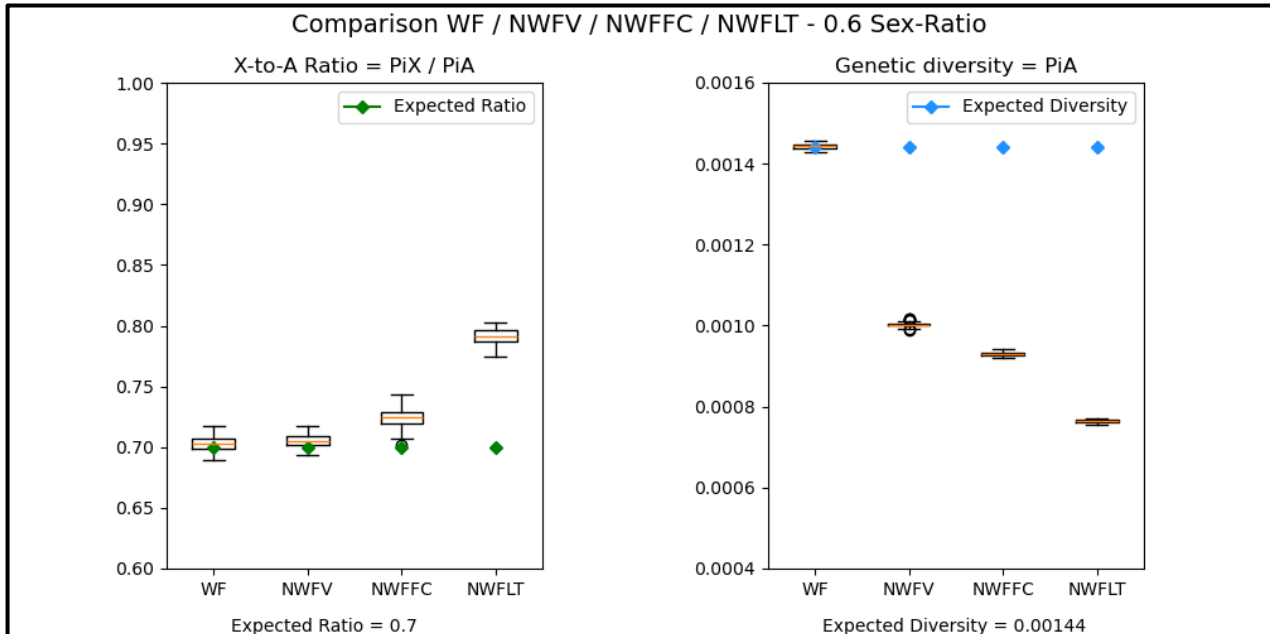
Effective Population size Autosome: 385
Effective Population size X: 319

Sex Ratio

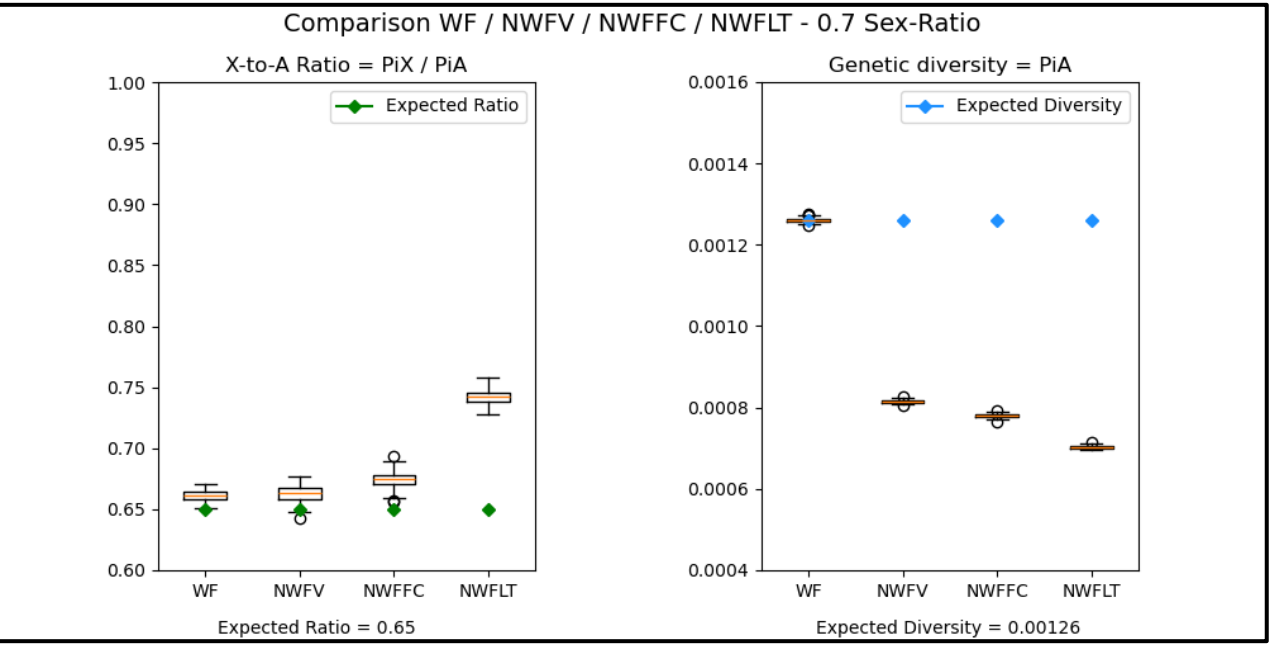

Comparison WF / NWFV / NWFFC / NWFLT - 0.25 Sex-Ratio
X-to-A Ratio = PiX / PiA
Expected Ratio
Expected Ratio = 0.875
Genetic diversity = PiA
Expected Diversity
Expected Diversity = 0.001125
WF
NWFV
NWFFC
NWFLT

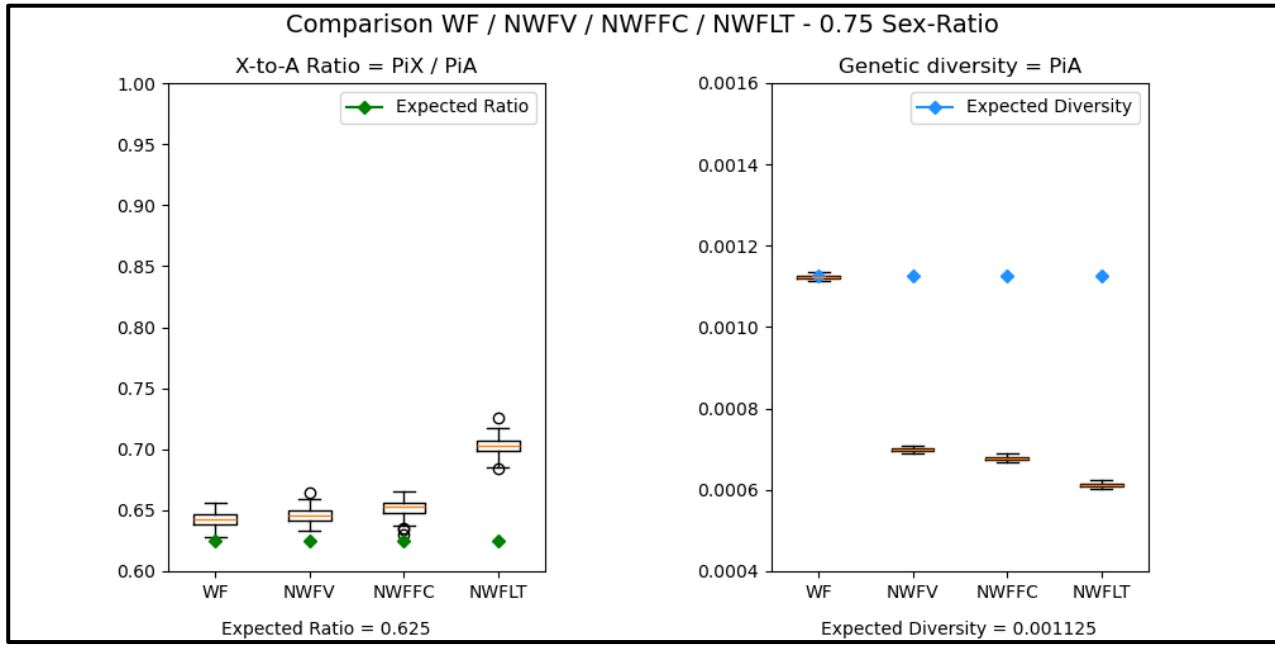

Comparison WF / NWFV / NWFFC / NWFLT - 0.3 Sex-Ratio
X-to-A Ratio = PiX / PiA
Expected Ratio
Expected Ratio = 0.85
Genetic diversity = PiA
Expected Diversity
Expected Diversity = 0.00126
WF
NWFV
NWFFC
NWFLT


Comparison WF / NWFV / NWFFC / NWFLT - 0.4 Sex-Ratio
X-to-A Ratio = PiX / PiA
Expected Ratio
Expected Ratio = 0.8
Genetic diversity = PiA
Expected Diversity
Expected Diversity = 0.00144
WF
NWFV
NWFFC
NWFLT

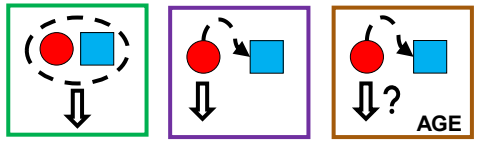

Comparison WF / NWFV / NWFFC / NWFLT - 0.6 Sex-Ratio
X-to-A Ratio = PiX / PiA
Expected Ratio
Expected Ratio = 0.7
Genetic diversity = PiA
Expected Diversity
Expected Diversity = 0.00144
WF
NWFV
NWFFC
NWFLT

Sex Ratio


Comparison WF / NWFV / NWFFC / NWFLT - 0.7 Sex-Ratio
X-to-A Ratio = PiX / PiA
Expected Ratio
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
WF
NWFV
NWFFC
NWFLT
Expected Ratio = 0.65
Genetic diversity = PiA
Expected Diversity
0.0016
0.0014
0.0012
0.0010
0.0008
0.0006
0.0004
WF
NWFV
NWFFC
NWFLT
Expected Diversity = 0.00126


Comparison WF / NWFV / NWFFC / NWFLT - 0.75 Sex-Ratio
X-to-A Ratio = PiX / PiA
Expected Ratio
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
WF
NWFV
NWFFC
NWFLT
Expected Ratio = 0.625
Genetic diversity = PiA
Expected Diversity
0.0016
0.0014
0.0012
0.0010
0.0008
0.0006
0.0004
WF
NWFV
NWFFC
NWFLT
Expected Diversity = 0.001125

Intrinsic Reproductive Skew Parameters NWF



Formula parmeters for each NWF models

	Nm	Nf	Rm	Rf	tm_mean	tf_mean
NWFV	4956	5044	9987.000000	9956.000000	2.055690	2.125099
NWFFC	5063	4937	10017.000000	9891.000000	2.061426	2.003443
NWFLT	3071	3271	9992.000000	10046.000000	9.311625	12.139101

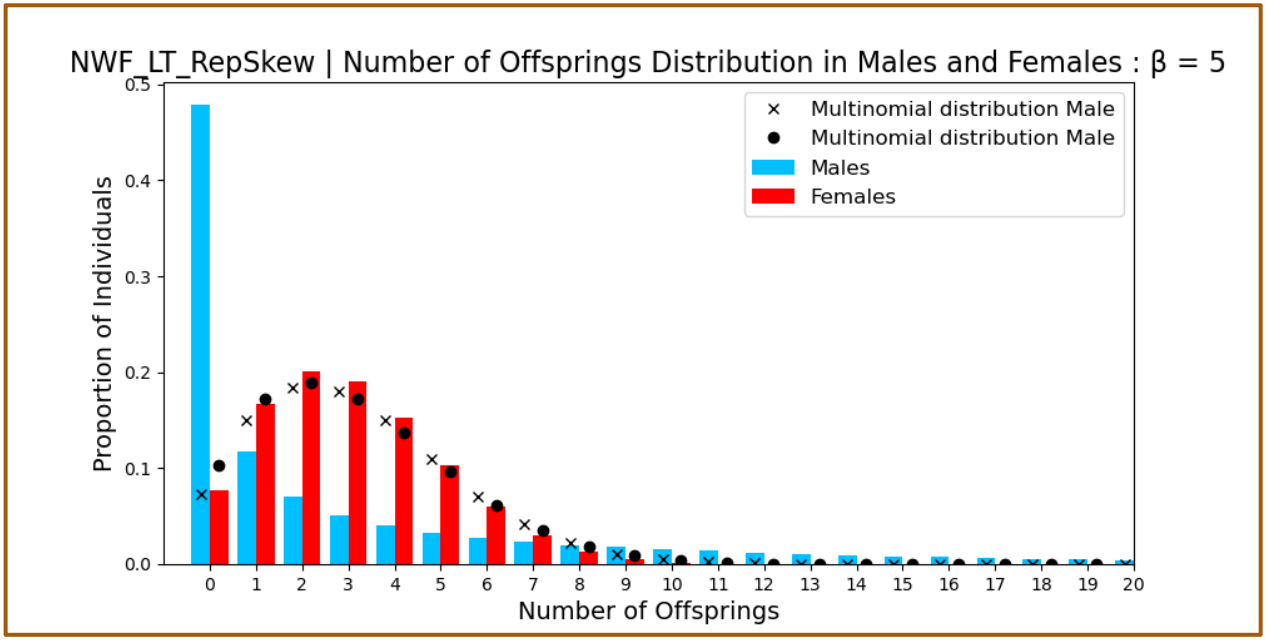
Reproductive Skew of males and females for border cases

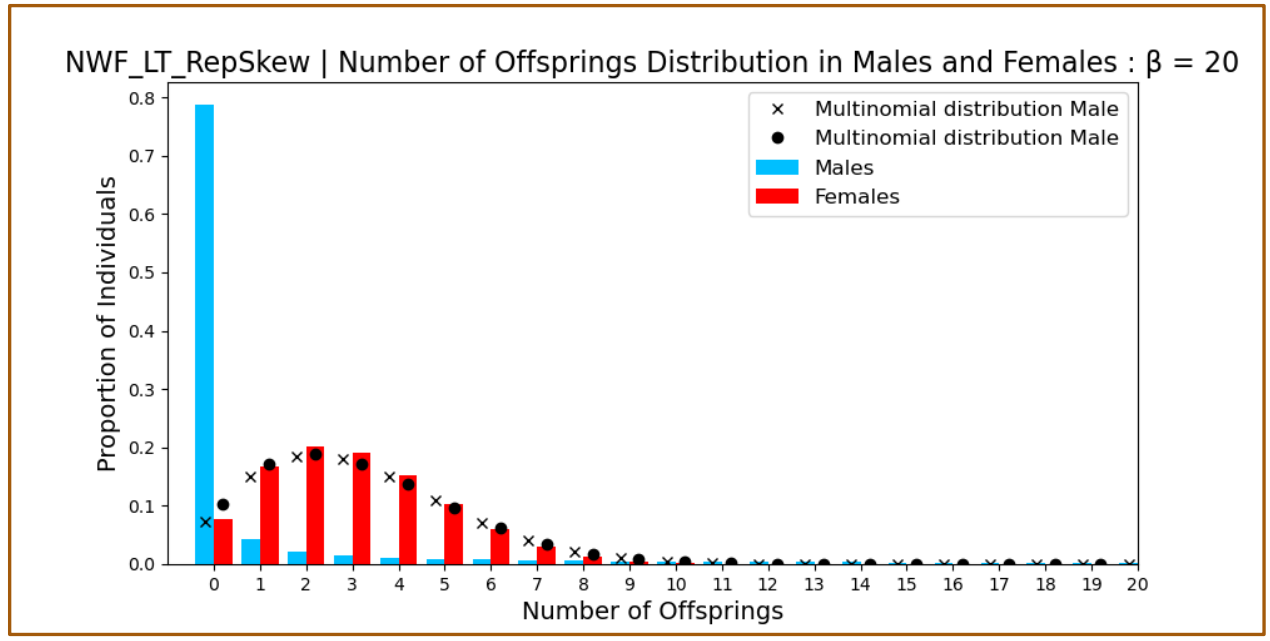
	Males	Females
All_Same	-0.250709	-0.249702
Multinomial	-0.000676	0.006649
1_Reproducer	4998.750651	4998.750143

Rep Skew NWF_LT

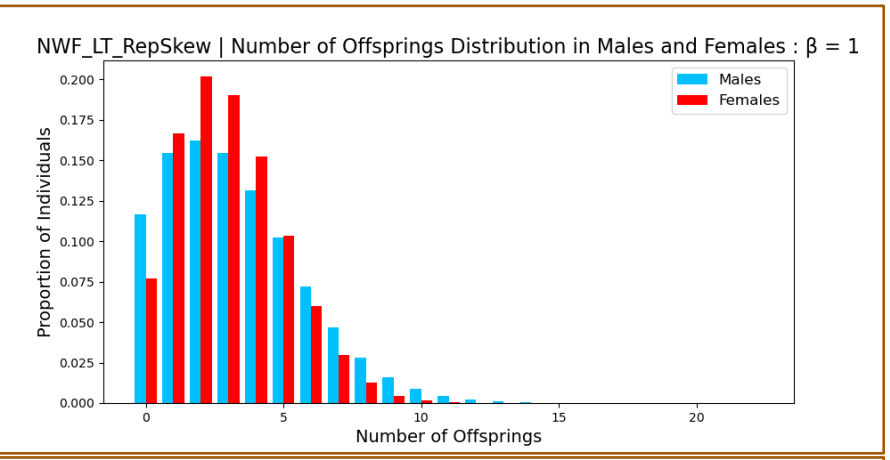
Formula parmeters for each value of Beta

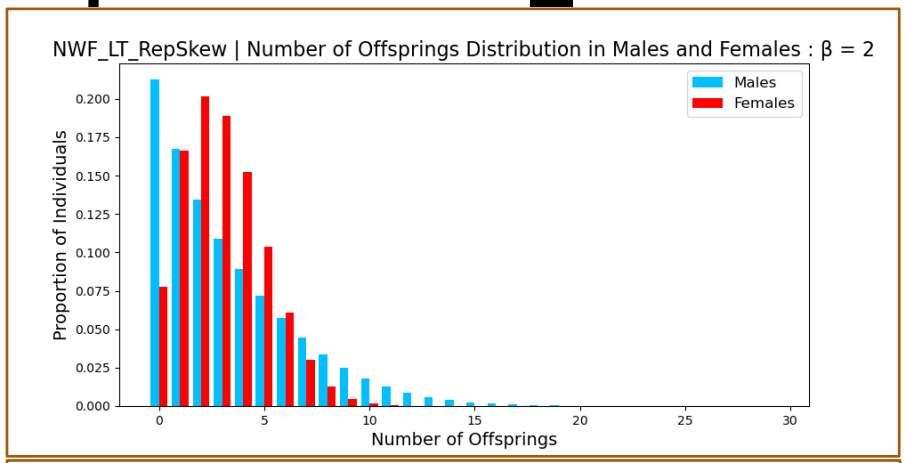
	Nm	Nf	Rm	Rf	tm_mean	tf_mean
β = 1	3076.142857	3275.591837	9987.877551	9738.816327	9.875586	12.498167
β = 2	3066.469388	3258.183673	9987.632653	9755.897959	9.780736	12.073126
β = 5	3040.224490	3247.591837	10001.040816	9734.653061	9.741480	12.514067
β = 10	3054.673469	3252.755102	9978.346939	9759.163265	9.786396	11.827307
β = 20	3039.714286	3259.367347	10001.428571	9754.265306	9.726230	12.670360
β = 40	3064.326531	3257.734694	9994.000000	9760.326531	9.774755	12.194951

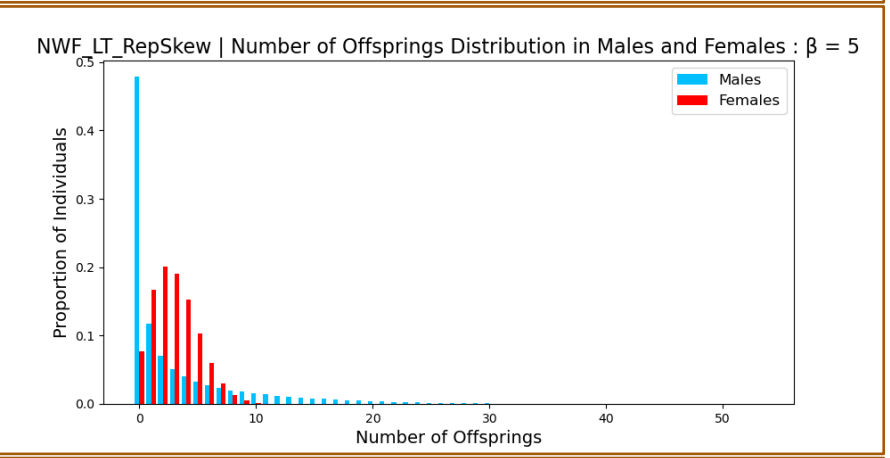


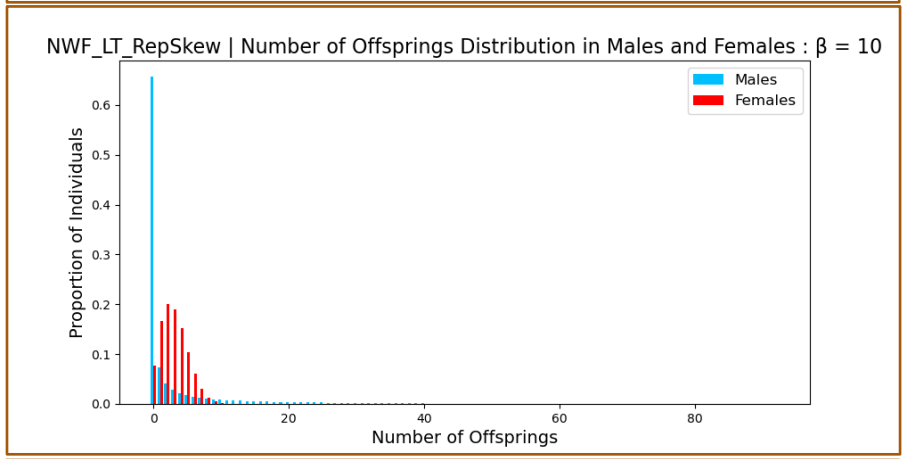


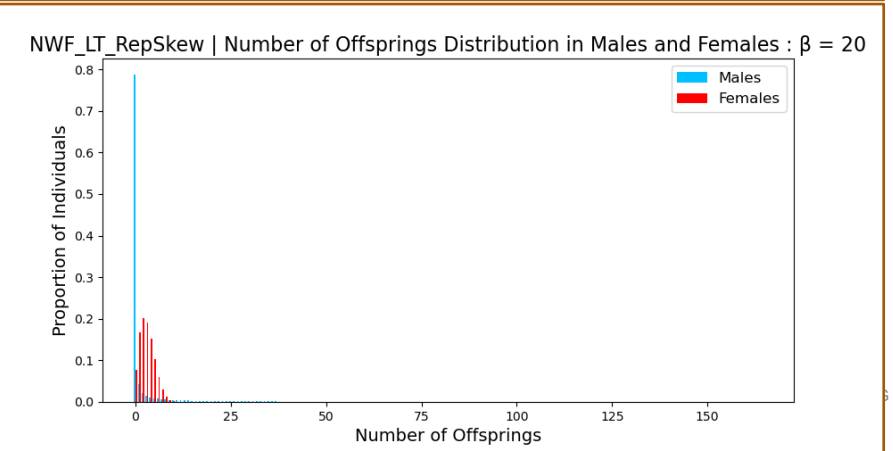
Rep Skew NWF_LT

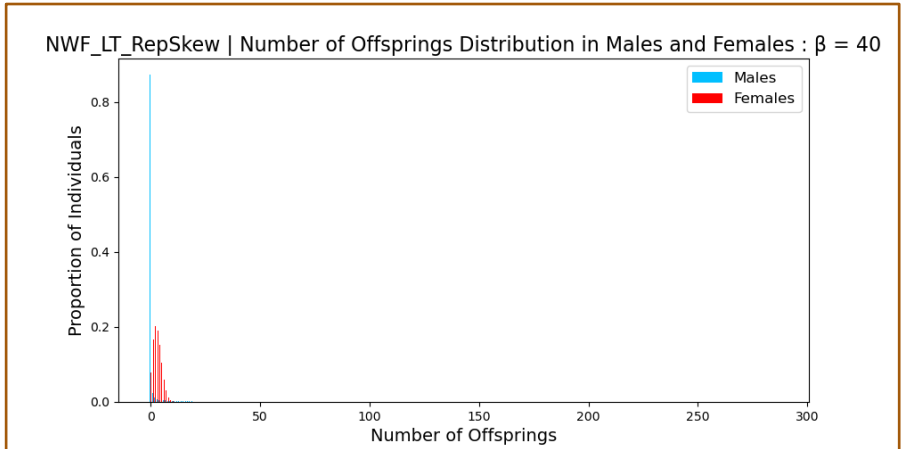






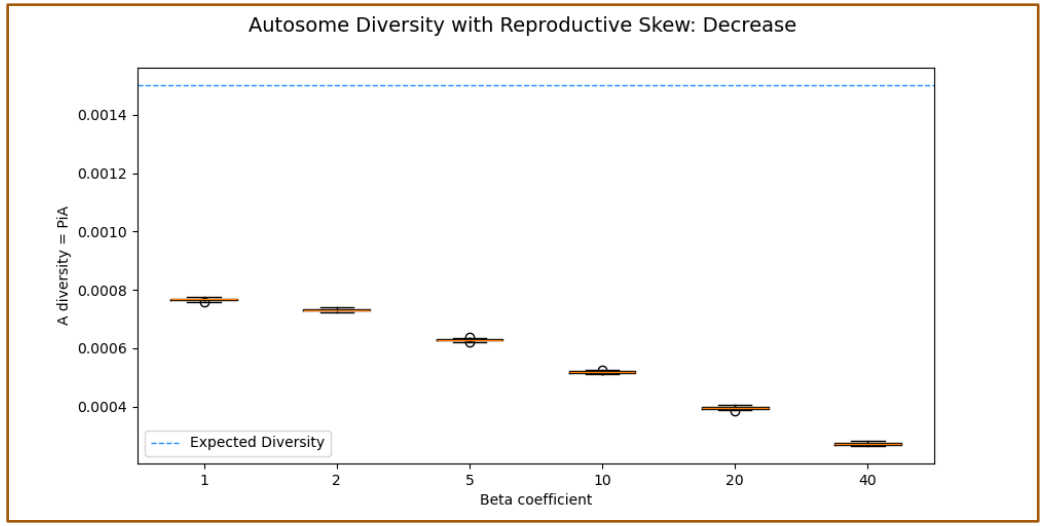


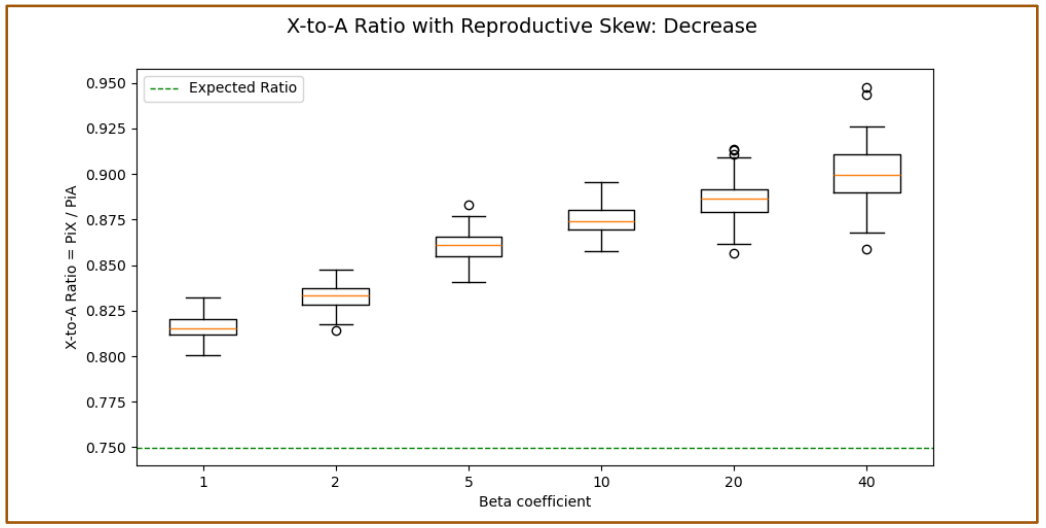




Beta	Noff Max
1	20
2	29
5	51
10	83
20	162
40	294

Rep Skew NWF_LT Decrease

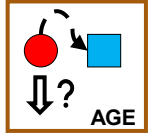




Reproductive Skew mean of males and females for each value of Beta: Decrease

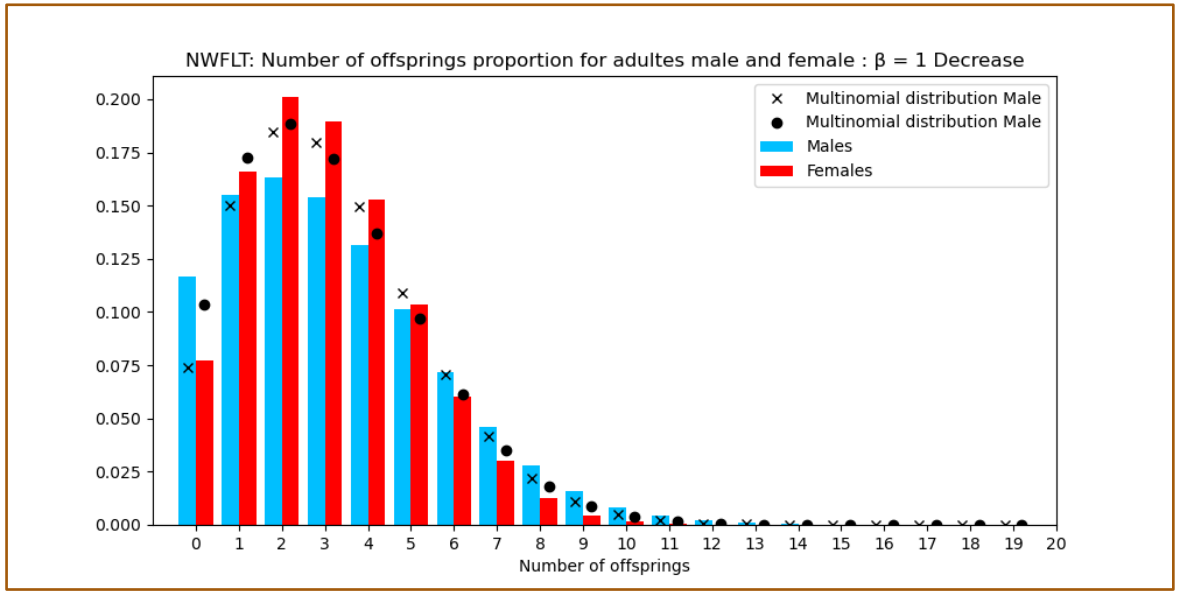
	Males	Females	Maximum	Minimum
β = 1	0.046982	-0.050898	3261.326531	-0.334301
β = 2	0.146017	-0.048585	3250.244898	-0.333697
β = 5	0.695122	-0.052516	3257.346939	-0.334396
β = 10	1.729548	-0.047915	3244.306122	-0.332676
β = 20	3.672025	-0.048948	3261.367347	-0.334740
β = 40	7.227717	-0.048275	3254.244898	-0.333976

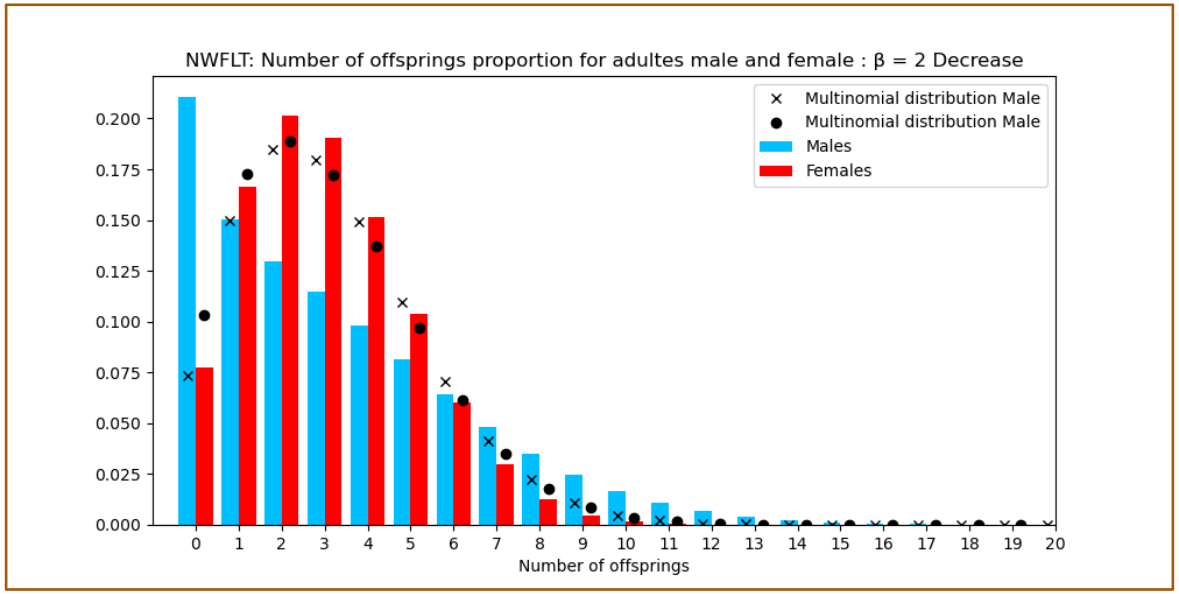
Rep Skew NWF_LT Decrease



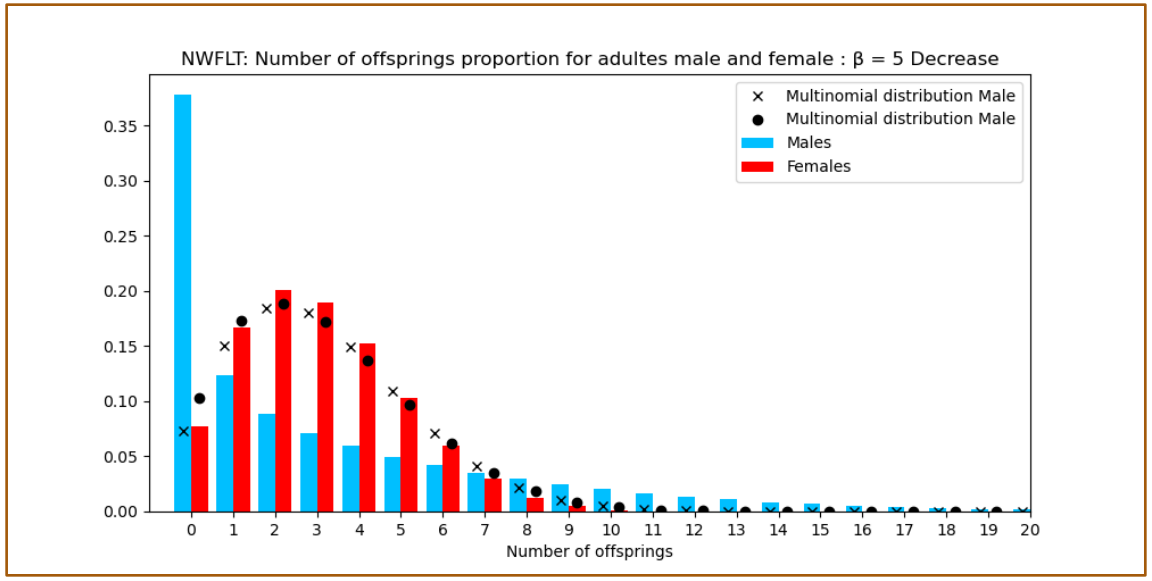
Formula parmeters for each value of Beta: Decrease

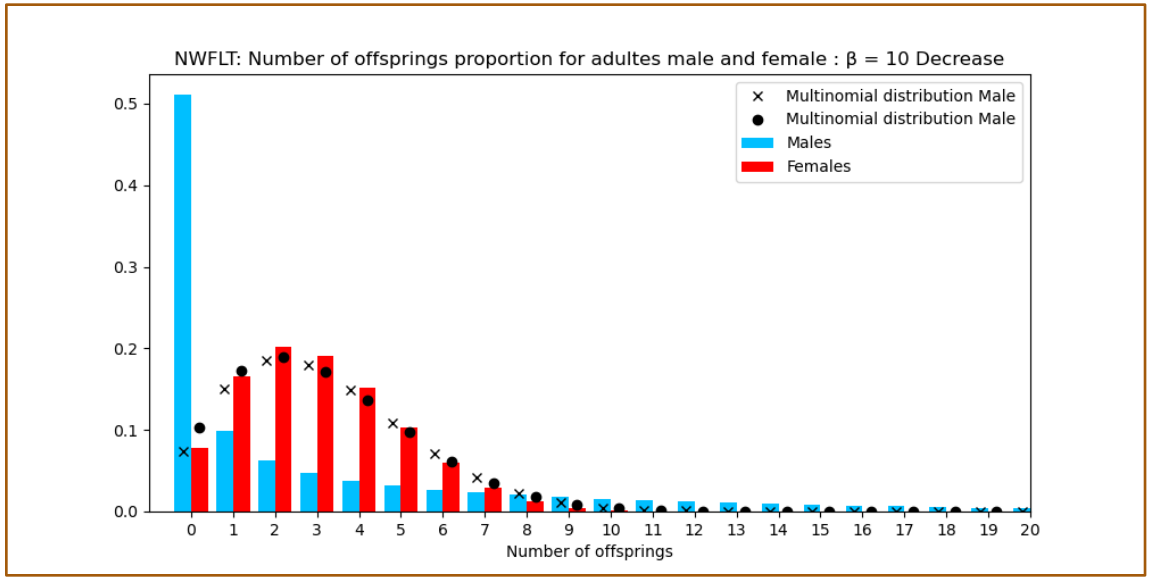
	Nm	Nf	Rm	Rf	tm_mean	tf_mean
β = 1	3053.020408	3261.326531	10002.857143	9755.673469	9.782063	12.632980
β = 2	3044.265306	3250.244898	9983.469388	9740.102041	9.712715	13.062518
β = 5	3052.040816	3257.346939	9978.897959	9740.979592	9.766386	12.181119
β = 10	3048.285714	3244.306122	9999.571429	9752.163265	9.734960	12.595074
β = 20	3052.938776	3261.367347	9998.040816	9743.000000	9.786502	12.685232
β = 40	3038.122449	3254.244898	9979.204082	9743.938776	9.745936	11.152510

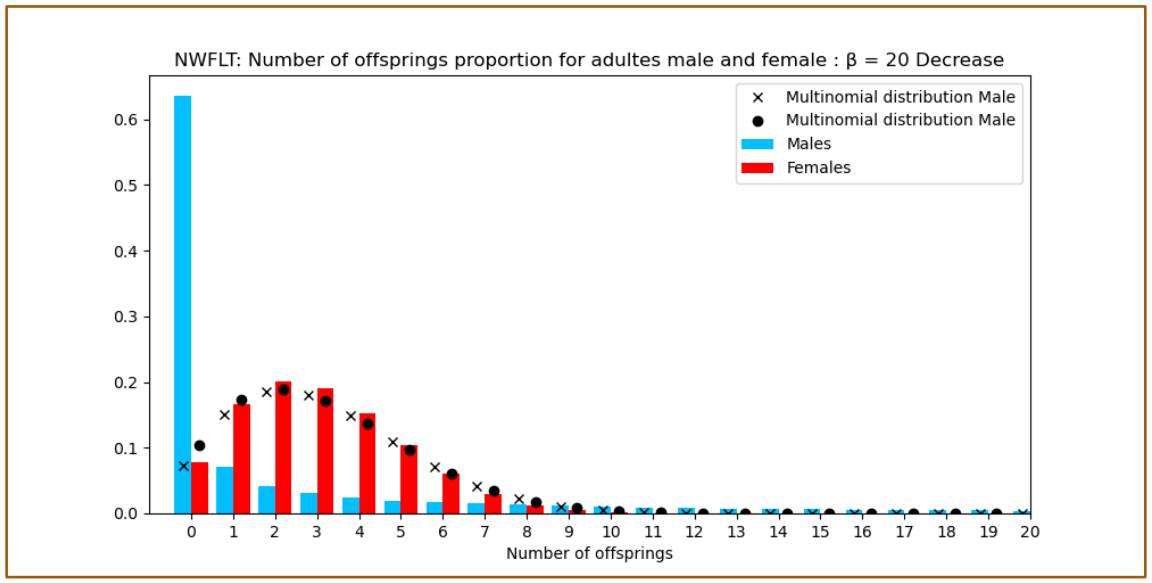


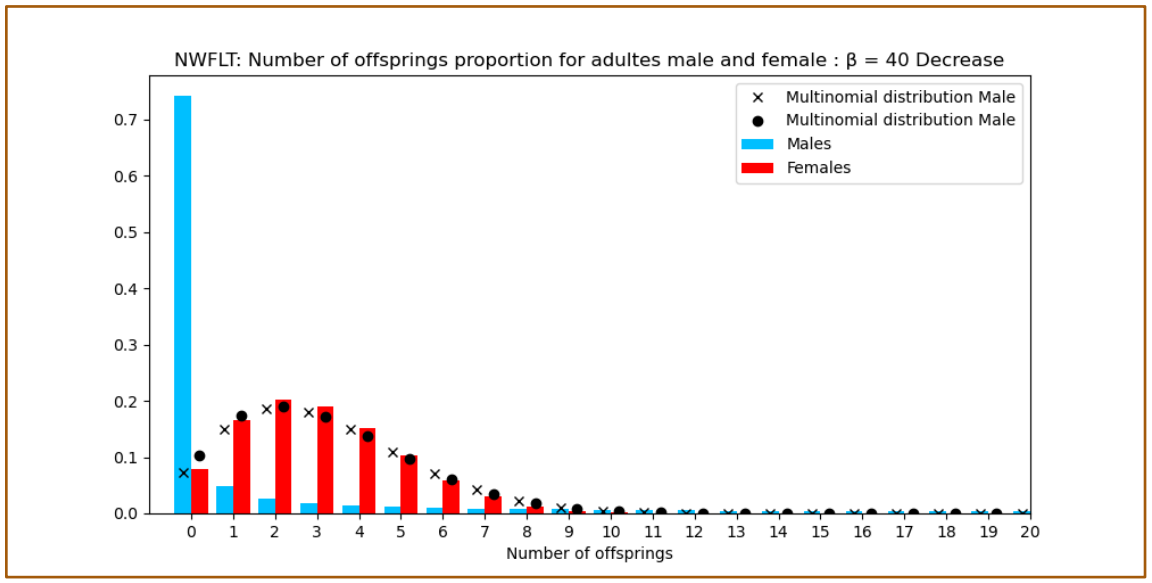


Rep Skew NWF_LT Decrease

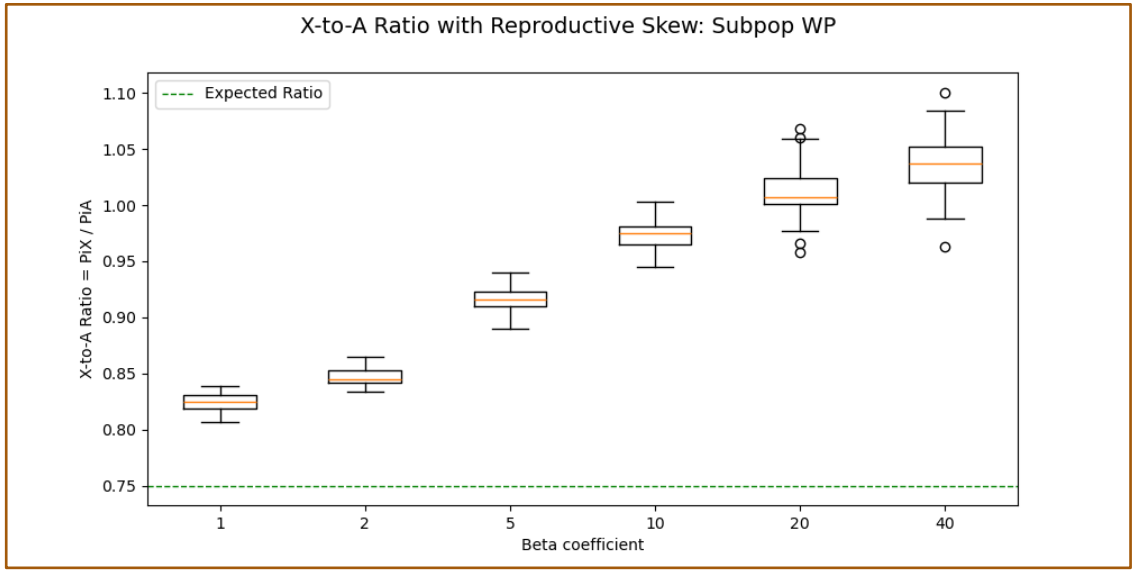


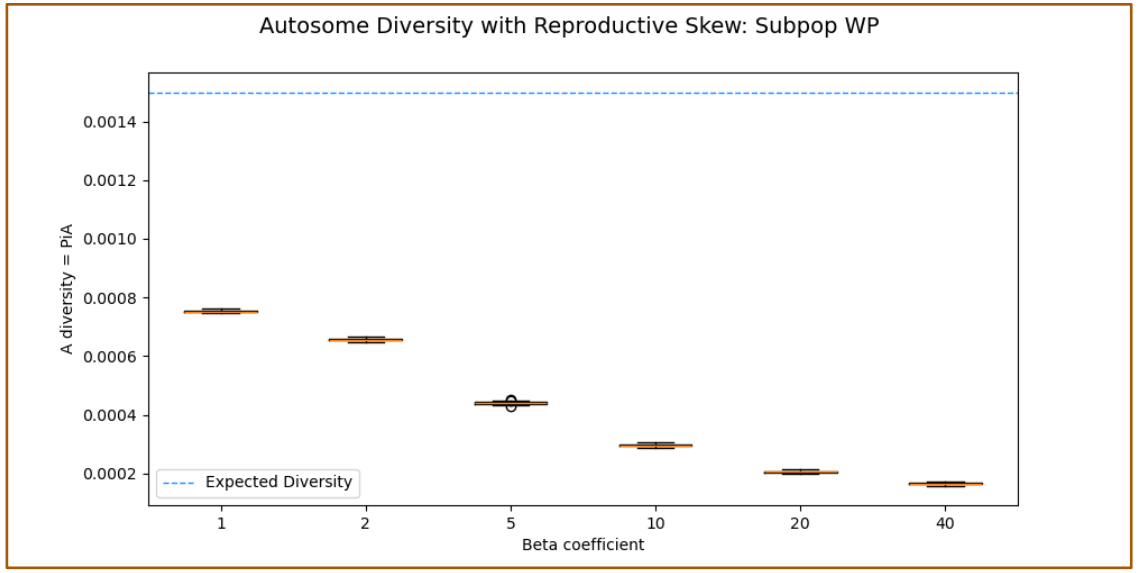






Rep Skew NWF_LT SubPop





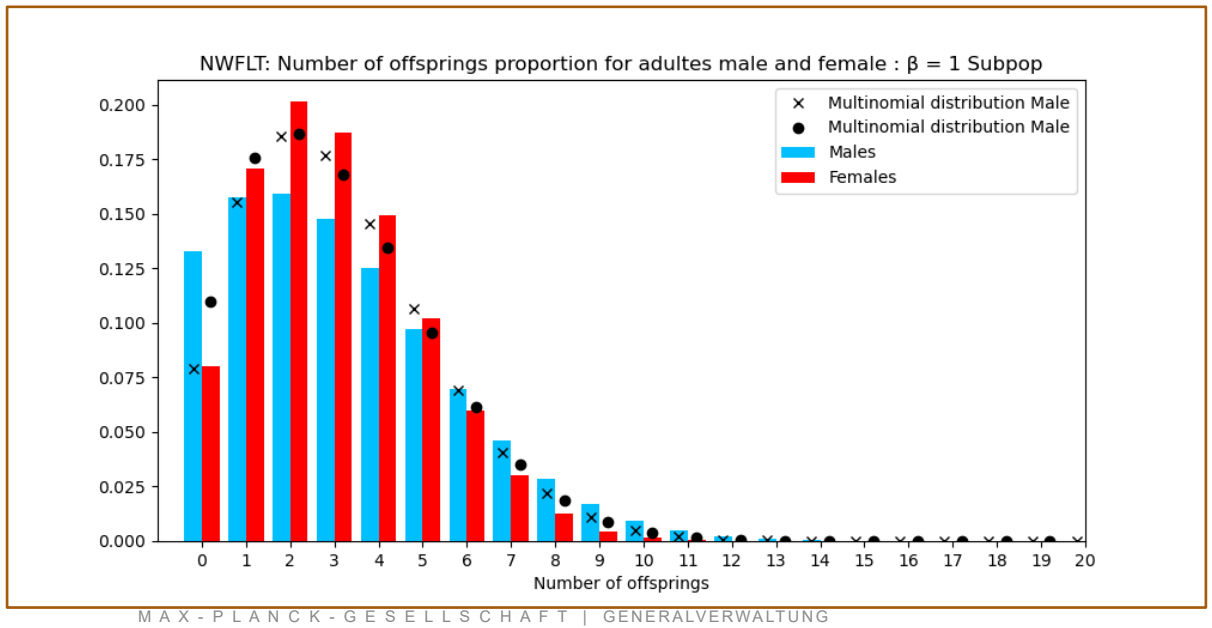
Reproductive Skew mean of males and females for each value of Beta: Subpop

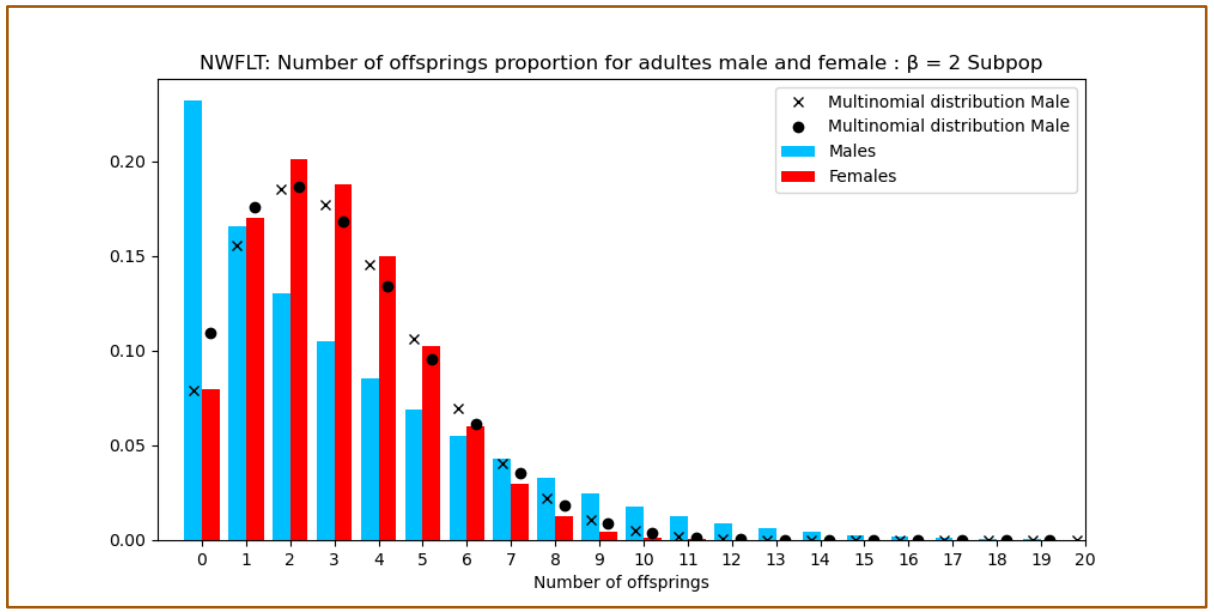
	Males	Females	Maximum	Minimum
β = 1	0.072780	-0.040937	46766.775510	-0.336031
β = 2	0.520975	-0.041227	46224.163265	-0.335896
β = 5	2.140844	-0.041697	46740.938776	-0.335986
β = 10	4.380227	-0.040755	26586.282609	-0.335513
β = 20	7.286294	-0.041101	46718.387755	-0.336089
β = 40	9.731268	-0.040946	40554.775510	-0.336164

Rep Skew NWF_LT SubPop

Formula parmeters for each value of Beta: Subpop

	Nm	Nf	Rm	Rf	tm_mean	tf_mean
β = 1	44266.224490	46766.775510	143078.510204	139173.795918	9.650354	12.447354
β = 2	43780.122449	46224.163265	141450.285714	137614.489796	9.654659	12.171369
β = 5	44231.673469	46740.938776	142987.163265	139115.714286	9.657500	12.363065
β = 10	25153.195652	26586.282609	81403.543478	79240.739130	9.630325	12.106171
β = 20	44207.326531	46718.387755	142919.959184	139005.918367	9.665760	12.429245
β = 40	38420.469388	40554.775510	123994.102041	120639.673469	9.664134	12.355166





Rep Skew NWF_LT SubPop