

File S3

Supporting Material on Simulation Methods

Age-structure

For the “long” age structure model, a fixed mean number of offspring per individual for each reproductive age-class was assigned to be 0.05556 males and 0.05556 females per mature female. For the “short” age structure model, the mean number of offspring per individual for each reproductive age-class was 0.68173 males and 0.68173 females per mature female. A key feature of this equilibrium age distribution is that the number of individuals in each age cohort is greater than or equal to the number of individuals in the next older age cohort. To achieve a stable population size in the “long” age structure, we set the probability of age-specific survival across a time-interval for juveniles and adults to be 0.946 and 0.980, respectively; maturity was reached after 20 breeding seasons. For the “short” age structure, the probability of age-specific survival across a time-interval for juveniles and adults was set at 0.767 and 0.5, respectively, and maturity was reached after 1 breeding season. The assumption of age-independent adult mortality is realistic for wild populations, where mortality is largely caused by extrinsic phenomena such as predation (Charlesworth 1994). A slight departure from the theoretical expectations for the numbers of individuals in each age class was required, in order to ensure whole numbers of individuals of each sex in the simulations.

With a constant population size, the mean age at reproduction for females is equal to $\sum xk(x) / \sum k(x)$, where x is age, and $k(x)$ is the probability of survival to age x times the fecundity at age x (formula 1.47a; Charlesworth 1994). In the “long” age structure simulations, fecundity is 0.05556 in adult age cohorts and zero in juvenile age cohorts. In the “short” age structure simulations, fecundity is 0.68173 in adult age cohorts and zero in juvenile age cohort. This provides an approximate generation time of 72.466 time units and 2.757 time units, respectively, for the “long” and “short” age structure simulations (Table S1). These generation times were used in the calculations for the theoretical expectations presented in Tables 1 and 2.

Life expectancy, which is the sum of the survival probabilities to each age class over all age classes (Charlesworth 1994) was lower than the generation time, and equal to 30.483 breeding seasons and 2.467 breeding seasons, respectively, for the “long” and “short” age structure simulations (Files S1 and S2). This shows that most individuals died without ever having reproduced in the “long” age structure, whereas most individuals did reproduce in the “short” age structure.

Mating systems

Following Nunney (1993), we treated harems as a special case of marriage, in which a group of females (as opposed to only one female) mate with one male each breeding season. Mate pairs produce a Poisson number of offspring of each sex, and offspring from each pair in a given breeding season are therefore full siblings. An excess of offspring is produced, and a randomly selected subset of these offspring, specified by the equilibrium age structure (see above), survive to become newborn individuals in the next breeding season. For the “monogamy” and “harem” models, before reproduction in each breeding season individuals from the youngest adult cohort (the “monogamy” models), or the youngest adult cohort plus all non-harem adult males (the “harem” models), are randomly assigned to any couples or harems that experienced death of a member at the end of the previous breeding season. Thus the death of a partner in a couple or harem does not limit the reproductive success of the survivor(s).

Inheritance in these simulations was Mendelian: each offspring received a randomly selected autosomal allele from each parent for each locus, a randomly selected X chromosome allele from their mother, and an X or Y allele from their father depending on whether the offspring was a daughter or son respectively. Mitochondrial DNA was inherited maternally.

Estimating N_e from simulations of genetic systems

The time taken to reach statistical equilibrium variation depends on N_e and μ . We performed preliminary simulations to explore what combination of population size and mutation rate allowed the population to reach equilibrium within a reasonable amount of time, while also minimizing variation in θ due to small population size. For the “long” age structure, we used a census size (N_c) of 1044 adults and 724 juveniles, and a mutation rate of 1.0776×10^{-5} mutations per gamete per time interval for the “long” age structure. For the “short” age structure, we used a census size (N_c) that was almost identical to the “long” age structure (1062 adults and 724 juveniles), and the mutation rate was set at 5.7551×10^{-6} mutations per gamete per time interval. Simulations were performed for intervals of 400,000 generations for the “long” age structure and 200,000 generations for the “short” age structure, and with 4,000 independent loci of each type (aDNA, xDNA, mtDNA, yDNA) for each social system. Plots of θ and the ratio of N_{e-x} / N_{e-a} , N_{e-mt} / N_{e-a} , and N_{e-y} / N_{e-a} over time (Figure S1) indicate that these conditions were sufficient for the populations to achieve mutation-drift equilibrium. These simulations are biologically unrealistic in the sense that a typical genome has effectively only one mtDNA and one yDNA locus but many aDNA and xDNA loci. However, independence allows us to obtain estimates of mean θ values with similar and maximal accuracy for each genetic system.

We inferred the population genetic parameter $\theta = 4N_e\mu$ from the mean level of heterozygosity at mutation – drift equilibrium. In these simulations, the mean H_{eq} was always < 0.03 , so we do not expect the non-linear relationship between H_{eq} and θ to substantially affect the relative values of our estimates of N_{e-a} , N_{e-x} , N_{e-mt} , and N_{e-y} .

Theoretical expectations

For the “long” age structure, x is equal to $58/522$ because 522 adult males collectively sire 58 offspring in a given breeding season and p is equal to $(1/522)$. For the “short” age structure, $x = 724/531$ because 531 males collectively sire 724 offspring each breeding season and $p = (1/531)$. With the “long” age structure, we have $p_1 = 58/522$ for simulations with a harem size of 9, because there are 58 harems and 522 adult males. With a harem size of 9, 58 harems, and 58 offspring produced by 522 females, $x_1 = 1$. When the harem size is 9 females per harem, ΔV_m for the “no storage” model and the “seasonal harem” model are relatively similar (i.e., 8.98 and 8.00, respectively). For the “short” age structure, $p_1 = 59/531$ and ΔV_m for the “no storage” model and the “seasonal harem” model are quite different (0.73 and 8.00, respectively). These calculations (Files S1 and S2) produce values that agree with those generated by formulae in Table 1 of Nunney (1993) for monogamous and harem social system. However, the formula for lottery polygyny in Table 1 of Nunney (1993) produces an estimate of N_e that corresponds to the case where $\Delta V_m = 1$. This discrepancy arises because his formula assumes a mean of two offspring per female, because generations are discrete, whereas in our case the mean number of offspring per capita for a single breeding season is not necessarily equal to two.

Testing the fit of jackknifed $N_{e,x}/N_{e,a}$ to theoretical expectations.

We used a permutation test to test whether the fit of the jackknifed $N_{e,x}/N_{e,a}$ ratios from the “harem for life” model to theoretical expectations with independent mate pairing was significantly worse than the fit of the jackknifed $N_{e,x}/N_{e,a}$ ratios from the “seasonal harem” model, based on simulations with harem sizes of 2, 3, 9, and 18 females per harem and the “long” age structure. The null hypothesis is that the jackknifed ratios were generated from the same distribution. We used as a test statistic the observed difference between the sum of the squared residuals from jackknifed $N_{e,x}/N_{e,a}$ ratios from each model. This statistic was compared to a distribution of statistics generated by combining the data and recalculating differences from random halves of the data 10,000 times. The P value of this test is equal to (10,000- the rank of the test statistic relative to this distribution) / 10,000.

Normality of θ with large sample size

Consider the ratio $H/(1 - H)$, where H is the mean heterozygosity over all sites.

The expectation and variance of the population value of H are $\mu = \theta/(1 + \theta)$ and σ^2 , respectively; with a mean over a large number of sites, m , and with small μ , σ^2 is approximately $\theta/3m$, the infinite sites value.

From the central limit theorem, when m is large (as here), H will be normally distributed. The question is whether $H/(1 - H)$ is approximately normal as well.

We have

$$d[H/(1 - H)]/dH = 1/(1 - H)^2 \quad (1)$$

so that
$$d^i[H/(1-H)]/dH^i = i!/(1 - H)^{i+1} \quad (2)$$

It follows that the Taylor’ series expansion of the deviation of θ from its expectation, $\delta\theta$, is given by:

$$\delta\theta = \sum_{i=1}^{\infty} \frac{(\delta H)^{i+1}}{(1 - \mu)^{i+1}} = \frac{\delta H}{(1 - \mu)^2 [1 - \delta H/(1 - \mu)]} \quad (3)$$

Since $\delta H \ll 1$, the variance of $H/(1 - H)$ is well approximated by:

$$V = \sigma^2/(1 - \mu)^4 \quad (4)$$

Now consider the 3rd moment of δH .

From Eqn. (3), we have:
$$E\{(\delta\theta)^3\} = E\{(\delta H)^3/(1-\mu)^6[1 - \delta H/(1-\mu)]^3\}$$

Since $\delta H \ll 1$, this can be approximated by:

$$E\{(\delta H)^3/(1-\mu)^6[1 - 3\delta H/(1-\mu)]\}$$

which is turn is approximately:

$$E\{(\delta H)^3[1 + 3(\delta H)/(1-\mu)]/(1-\mu)^6\}$$

Given that H is normally distributed, so that its odd moments about its mean are zero, this gives:

$$M_{3_s} = 3M_{4H}/(1-\mu)^7 \quad (5)$$

where M_{3_s} is the 3rd moment of θ about its mean, and M_{4H} is the 4th moment of H about its mean, which is equal to $3\sigma^4$. The skewness of θ , S_s , is measured by the ratio of M_{3_s} to $V_s^{3/2} = \sigma^3/(1-\mu)^6$:

$$S_s = 9\sigma/(1-\mu) \quad (6)$$

Given that σ is of order $1/\sqrt{m}$, the skewness is $\ll 1$ for large m , as in this case.

Similarly,

$$E\{(\delta\theta)^4\} = E\{(\delta H)^4/(1-\mu)^8[1 - \delta H/(1-\mu)]^4\}$$

which can be approximated by:

$$E\{(\delta\theta)^4\} = E\{(\delta H)^4/[1 + 6(\delta H)^2/(1-\mu)^2](1-\mu)^8\}$$

i.e.

$$\begin{aligned} M_{4_s} &= [M_{4H}/(1-\mu)^8] + [6M_{6H}/(1-\mu)^9] \\ &= [3\sigma^4/(1-\mu)^8] + [90\sigma^6/(1-\mu)^9] \end{aligned} \quad (7)$$

The kurtosis of θ is measured by $K_s = M_{4_s}/V_s^2 - 3$, so that:

$$K_s = [90\sigma^2/(1-\mu)] - 3 \quad (8)$$

Again, since σ is $O(1/m)$, this approaches zero for large m .