EFFECTIVE POPULATION SIZE

Assumptions of the Hardy-Weinberg model include the following:

1. Mating is random (i.e., gametes from all individuals in the population have an equal probability of being represented in the next generation)
2. The sex ratio is equal.
3. Generations are not overlapping.

These assumptions are rarely met in real populations.

EFFECTIVE POPULATION SIZE (Ne) – the size of an ideal population that would have the same rate of inbreeding or decrease in genetic diversity by genetic drift as the real population being considered.

IDEAL POPULATION – A genetically ideal population is defined as one in which all individuals in the population have an equal probability of being the parents of any individual in the next generation. In other words, a genetically ideal population should be closed and without overlapping generations, and all individuals should mate completely at random. Obviously such a population exists only in the mind of theoreticians. In order to represent the extent to which a real population differs from the ideal, Sewall Wright (1931) developed the concept of genetically effective population size.

CALCULATIONS OF Ne ARE COMPLEX!

For detailed discussion of effective population size, look at a population genetics book. There are several in the Marston Science Library. We will only examine a few simple ways to calculate an approximate Ne. Before attempting to conduct research involving calculations of Ne, it would be essential for you to dig much deeper into the literature on effective population size.

Example of calculation of Ne for grizzly bears in Yellowstone area (taken from Brussard 1986):


*Note: Fortunately, grizzly bear populations have increased since Brussard (1986) wrote this article.
1. **Effects of age structure on Ne**

Ne = G (Ni)

G = generation length, which is the average time elapsing between the births of mothers and the births of their daughters. 

\[ \frac{\left( \sum l_x m_x x \right)}{\left( \sum l_x m_x x \right)} \]

\( l_x \) = the probability of surviving to age x

\( m_x \) = the expected number of female offspring per female in each age group

\( x \) = age

Ni = number of individuals produced per year that survive to reproductive age

**Demographic estimates for grizzly bears:**

- G = 10.25 years for grizzly bears
- 36 females of reproductive age in population at time of study
- Females reproduce about every 3 years
- Mean of 1.9 cubs per litter
- Probability of a cub’s surviving to reproductive age (5 years) = 0.25

36 females/3 years time between reproduction = 12 reproducing females per year on average

12 females × 1.9 cubs per litter = 22.8 cubs per year on average

\[ Ni = (12 \text{ females reproducing per year}) \times (1.9 \text{ cubs per litter}) \times (0.25 \text{ probability of survival to reproductive age}) \]

\[ Ni = (12)(1.9)(0.25) = 5.7 \]

\[ Ne = 10.25 \times (5.7) = 58 \]

Total estimate of grizzle bears in Yellowstone area (i.e., actual population size Na) = 245

\[ Ne / Na = 58 / 245 = 0.24 \text{ or } 24 \text{ percent} \]

Based only on age structure, effective population size is about ¼ of total population.
2. **Effects of Fluctuations in Population Size on Ne**

\[ Ne = \frac{t}{(1/N_1) + (1/N_2) + \ldots (1/N_t)} \]

10.25 years equals one generation

\[ t = \text{number of generations} \]

\[ N_1 = \text{population at time 1} \]

\[ N_2 = \text{population at time 2, etc.} \]

Grizzly population size (censused): \( \approx 8 \) generations


Guess population size for this problem

1930 – 150 bears; 1950 – 200 bears

\[ Ne = \frac{8}{1/40 + 1/150 + 1/260 + 1/200 + 1/154 + 1/202 + 1/136 + 1/200} = 124 \]

Mean \( Na = \frac{40+150+260+200+154+202+136+200}{8} = 167 \) \( Ne/\text{Mean } Na = 124/167 = 0.74 \)

Ne considering only population fluctuations is 74% of the average censused population (mean \( Na \)).

3. **Inbreeding Effects on Ne**

\[ F = \text{inbreeding coefficient} \]

\[ H = \text{actual heterozygosity} \]

\[ H_0 = \text{expected heterozygosity} \]

\[ F = \frac{H_0 - H}{H_0} \]

\[ Ne = \frac{Na}{1 + F} \]

Definitions of \( F \):

1. a measure of the extent to which mating individuals are more closely related than individuals drawn at random from the population
2. fractional reduction in heterozygosity in the actual population as compared to a random-mating (ideal) population.

No data on \( F \) are available for grizzlies. Average inbreeding in all known populations of birds and mammals = 2%. \( Na = 245 \) grizzly bears.

Using this figure:

\[ Ne = \frac{245}{1 + 0.02} = 240 \]

considering only the effects of inbreeding.
3. **Effects of Variance in Progeny Number on Ne**

**Example with blackfooted ferrets**

These ferrets are highly endangered and have been the subject of intensive captive breeding.

\[
\text{Ne} = 4 \left( \frac{\text{Na}}{(\sigma^2 + 2)} \right) \quad \text{X}_i = \text{No. offspring of female i}
\]

Variance in progeny number:

\[
\sigma^2 = \frac{\sum (x_i - \mu)^2}{N_F}
\]

\(\mu = \text{average of all females for number of offspring}\)

\(N_a = \text{number in census population}\)

\(N_F = \text{number of females}\)

*Assume \(N_a = 10\) and \(N_F = 5\)

<table>
<thead>
<tr>
<th>♀</th>
<th># young</th>
<th>((x_i - \mu)^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>((1 - 4.6)^2) = 12.96</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>((2 - 4.6)^2) = 6.76</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>((4 - 4.6)^2) = 0.36</td>
</tr>
<tr>
<td>4</td>
<td>8</td>
<td>((8 - 4.6)^2) = 11.56</td>
</tr>
<tr>
<td>5</td>
<td>8</td>
<td>((8 - 4.6)^2) = 11.56</td>
</tr>
</tbody>
</table>

Total = 23

\[43.2 \div 5 = 8.64 = \sigma^2\]

Mean number of young per female

\((\mu) = 23 \div 5 = 4.6\)

\[\text{Ne} = \left[ 4 \left( \frac{10}{(\sigma^2 + 2)} \right) \right] = 40 / 10.64 = 3.76\]

To see how progeny number affects Ne, compare the Ne above to the Ne below.

<table>
<thead>
<tr>
<th>♀</th>
<th># young</th>
<th>(\sigma^2)</th>
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<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>2.96</td>
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<tr>
<td>2</td>
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<tr>
<td>4</td>
<td>3</td>
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<tr>
<td>5</td>
<td>6</td>
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\[\text{Ne} = 40 / (2.96 + 2) = 8.06\]
5. **Effects of Sex Ratio on Ne**

**Hypothetical Prairie Dog Towns**

Na (actual pop. size) = 10

\[
Ne = \frac{4 N_m N_f}{(N_m + N_f)}
\]

For Na = 10:

\[
\frac{4(2)(8)}{2 + 8} = 6.4 \text{ Ne}
\]

For Na = 50:

\[
\frac{4(10)(40)}{50} = 32 \text{ Ne}
\]

For Na = 100:

\[
\frac{4(20)(80)}{100} = 64 \text{ Ne}
\]

Examples of management practices that affect Ne:

Bag limits that skew sex ratio (e.g., bucks-only hunting)

\[
Ne = \frac{4 N_m N_f}{(N_m + N_f)}
\]

\(N_m\) = number of males that mate

\(N_f\) = number of females that mate

Assume: 100 bucks and 900 does

\[
Ne = \frac{4(100)(900)}{1000} = 360
\]
Rate of Loss of Heterozygosity with Genetic Drift:

\[ H_t = (1 - \frac{1}{2Ne})^t (H_0) \]

* Each generation heterozygosity is reduced by \( \frac{1}{2Ne} \)

\( H_t \) = heterozygosity remaining after \( t \) generations.
\( H_0 \) = initial heterozygosity

For \( Ne = 50 \)

\[ H_1 = \left( 1 - \frac{1}{(2)(50)} \right)^1 H_0 \]
\( H_1 = H_0 - 0.01 H_0 \)

After one generation the decrease in heterozygosity = 1% (assumes no selection, mutation…)
Tolerance of 1% loss of heterozygosity per generation is an animal breeding standard. After 100 generations if population remains at 50, 74% of the heterozygosity will have been lost.

For \( Ne = 500 \)

\[ H_1 = \left( 1 - \frac{1}{(2)(500)} \right)^1 H_0 \]
\( H_1 = H_0 - 0.001 H_0 \)

After one generation the decrease in heterozygosity = 0.1% (assuming no selection, mutation…).

These relationships are the basis of the 50/500 rule for minimum viable populations based on genetic criteria (Franklin 1980). Rationale as follows:

- \( Ne \) of 50 is short-term goal to prevent inbreeding depression (corresponds to 1% inbreeding per generation tolerated by animal breeders)

- \( Ne \) of 500 is long-term goal that will balance genetic variation created by mutation with that lost by genetic drift (Note: recent work suggests that mutation may not balance drift in this population size.)

The aim of the 50/500 rule is to provide a number above which populations are safe, below which they face unacceptable risk of extinction. Do you have confidence in this rule? It has been used extensively in conservation planning for wildlife, so you should understand how the “rule” was derived. Recent work suggests that \( Ne \) must be much larger (on the order of 1000s of individuals for long term persistence).