

## **Group Selection, Population Structure, Shifting Balance**

Note: For next time read Saetre et al. *Nature*.

Group selection: differential survival and reproductive success of different groups in structured populations.

Note: this is not the same as the "Group Selection" invoked by VC Wynn-Edwards, which implied a "good of the species" effect. The same "good of the species" conventional wisdom was used by medical doctors to explain the evolution of benign parasites. That reasoning has been rejected.

The modern view of group selection is that different groups may be more productive, and that may affect the course of natural selection. Groups are viewed as a "level of selection," like genes and individuals.

But does it work? This is controversial. Suppose we had 5 groups, with different trait means. Suppose the difference was correlated with total group productivity. Some graphs... Examples...

## Shifting balance

Remember the sickle cell anemia case? Inbreeding changed the adaptive topography, leading selection to take the population to a higher fitness peak.

Here we want to consider peak shifts without changing the adaptive surface. We do it in the context of the argument between RA Fisher and Sewel Wright.

Fisher's view.

1. Populations are large and panmictic\*

a) hence genetic drift and inbreeding are not important

b) selection operates on the average additive effect of alleles

\*"...I believe that  $N$  must usually be the total population on the planet."

"The population is conceived to contain all the genetic combinations possible with frequencies appropriate to their actual probabilities of occurrence" in all environmental circumstances.

## Sewel Wright's view

1. Populations are subdivided into subpopulations (demes).
  - a) inbreeding and drift cannot be ignored
  - b) selection operates on combinations of alleles within demes. Epistasis cannot be ignored.

## Wright's Shifting Balance of Genetic Drift and Natural Selection

Phase 1. Genetic drift is small, semi-isolated populations allows the crossing of fitness valleys. (Remember that selection is weaker in the vicinity of local adaptive peaks. And that drift outweighs selection when  $s < 1/Ne$ )

Phase 2. Selection within demes causes movement up adaptive peaks, after crossing a fitness valley

Phase 3. Interdemic selection. Demes at higher fitness peaks export more migrants. Migrants from high-fitness demes can move low-fitness demes across fitness valleys.

Groups: what are three plusses and three minuses regarding Wright's theory of shifting balance?

Why is shifting balance so controversial?\*

Genetic drift will depend on **Effective Population Size:  $N_e$** .

S. Wright's definition of effective population size ( $N_e$ ):

**"the number of breeding individuals in an idealized population that would show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration".**

$N_e$  is affected by lots of things, including

1. variance among families in offspring (o) production

$$N_e = \frac{N-1}{\left( \frac{\text{var}_{(o)}}{\bar{x}_{(o)}^2} + \frac{1}{\bar{x}_{(o)}} \right)}$$

2. Variance in N over time:

$$\frac{1}{N_e} = \frac{1}{t} \sum_{i=1}^t \frac{1}{N_i} = \text{harmonic mean}$$

thus  $N_e = \frac{1}{\text{harmonic mean}}$

3. Unequal sex ratio:

$$N_e = \frac{4N_{\text{females}}N_{\text{males}}}{N_{\text{females}} + N_{\text{males}}}$$

see worked examples

- \*1. phase 1 and 3 may be in conflict.
- 2. coadapted gene complexes in migrants broken up by recombination.
- 3. do high-fitness demes export more migrants?

Below : the effective population size is affected by the variance in the number of offspring produced per family. We assume at carrying capacity, that the mean number of offspring per family is equal to 2. We set  $N = N_{\text{actual}} = 100$ . Now we change the variance.

First consider the case where all families produce 2 offspring. Hence the variance = 0. Note: The effective population size is (two times) greater than the actual population size. In other words, in a population genetic sense the population behaves as if it is twice as large ( $N_e = 198$ )

```
In[388]:= Ne =  $\frac{N_{\text{actual}} - 1}{\frac{\text{var}}{\text{mean}^2} + \frac{1}{\text{mean}}}$ ;
```

```
Nactual = 100;  
mean = 2;  
var = 0;
```

```
Ne
```

```
Out[392]= 198
```

Now we let the mean equal the variance equal to 2. Thus the variation among families is just random (this is the case when  $\text{var}=\text{mean}$ ).

Note that the effective population size is very close (99) to the actual population size (100).

```
In[393]:= Ne = .  
Nactual = .  
var = .  
mean = .  
Ne = .  
Ne =  $\frac{N_{\text{actual}} - 1}{\frac{\text{var}}{\text{mean}^2} + \frac{1}{\text{mean}}}$ ;
```

```
Nactual = 100;  
mean = 2;  
var = 2;
```

```
Ne
```

```
Out[402]= 99
```

Finally, we let the variance be larger than the mean, which would be expected if there is among family variance due to selection.

Note that the effective population size is much lower than the actual population size. Selection has decreased the effective population size to 66.

```
In[403]:= Ne = .
Nactual = .
var = .
mean = .
Ne = .

Ne = 
$$\frac{Nactual - 1}{\frac{var}{mean^2} + \frac{1}{mean}};$$


Nactual = 100;
mean = 2;
var = 4;

Ne
```

Out[412]= 66

Now we consider the effect of the operational sex ratio on  $N_e$ .

First let's have Number of females = Number of males = 50.

The effective population size is 100, same as the actual population size.

```
In[413]:= Ne = .
Nactual = .
var = .
mean = .
Ne = .

Ne = 
$$\frac{4 Nfem Nmales}{Nfem + Nmales};$$


Nactual = 100;
Nfem = 50;
Nmales = 50;

Ne
```

Out[422]= 15.36

In[439]:=

Now let's have Number of females = 96, and the Number of males = 4.

The effective population size is 15.36, same as the actual population size.

```

In[423]:= Ne = .
Nfem = .
Nmales = .
var = .
mean = .
Ne = .
Ne =  $\frac{4 Nfem Nmales}{Nfem + Nmales}$ ;

Nfem = 96.0;
Nmales = 4.0;

FullSimplify[Ne]

```

Out[432]= 15.36

Finally, we consider the effect of variance in N over time.

First no variance : N at time 1 = N at time 2 = 100. Remember that  $1/Ne$  is equal to the harmonic mean of N. That is

$$\frac{1}{N_e} = \frac{1}{t} \sum_{i=1}^t \frac{1}{N_i}$$

```

In[433]:= Ne = .
harmonicmean =  $\frac{1}{2} \left( \frac{1}{100} + \frac{1}{100} \right)$ 

```

Out[434]=  $\frac{1}{100}$

```

In[435]:= Ne = 1 / (harmonicmean)

```

Out[435]= 100

Now let N be variable over the two time periods : N at time 1 = 150; N at time 2 = 50. Remember that  $1/Ne$  is equal to the harmonic mean of N.

Note that the effective population size is equal to 75, which is much closer to the lower value observed at time 2. the harmonic mean tends to weight lower values more.

```

In[436]:= Ne = .
harmonicmean =  $\frac{1}{2} \left( \frac{1}{150.0} + \frac{1}{50.0} \right)$ 

```

Out[437]= 0.0133333

```

In[438]:= Ne = 1 / (harmonicmean)

```

Out[438]= 75.