I. Defining Fitness

What is fitness?

Imagine a simple case where a population consists of individuals who have phenotype z_1 and individuals who have phenotype z_2. The offspring of these individuals always have a phenotype identical to their parent. What determines which of these individuals ultimately predominates within the population?

Case 1: Annual organisms

Assume individuals survive to reproduce with probability *l*(z) and that surviving individuals produce, on average, *m*(z) offspring. How do the relative frequencies of the types change over time?

Start by determining the number of individuals of each type in the next generation:

$$N'(z_1) = l(z_1)m(z_1)N(z_1) = W(z_1)N(z_1) \tag{1a}$$

$$N'(z_2) = l(z_2)m(z_2)N(z_2) = W(z_2)N(z_2) \tag{1b}$$

What do equations (1) tell us about the fate of the two phenotypes?

$$N_t(z_1) = W^t(z_1)N_0(z_1) \tag{2a}$$

$$N_t(z_2) = W^t(z_2)N_0(z_2) \tag{2b}$$

- ⇨ The quantity W entirely determines the relative abundances of the two phenotypes at any point in the future and is thus a complete description of fitness

Conclusion: For annual organisms, the change in frequencies of types depends on only the product of the survival and fertility of the types. Thus, NS may favor decreased fertility or decreased survival if doing so increases their product (fitness) through the presence of fundamental <u>life history trade-offs</u>

Case 2: Fitness in organisms with age structure

Assume individuals survive to age x with probability l_x and produce an expected number of offspring equal to m_x in age x. How do the relative frequencies of the types change over time?

Phenotype z_1

x	l_x	m_x	$l_x m_x$
1	**1.00**	**0.00**	**0.00**
2	**0.75**	**0.00**	**0.00**
3	**0.50**	**1.00**	**0.50**
4	**0.25**	**4.00**	**1.00**

Phenotype z_2

x	l_x	m_x	$l_x m_x$
1	**1.00**	**1.00**	**1.00**
2	**0.75**	**0.67**	**0.50**
3	**0.00**	**0.00**	**0.00**
4	**0.00**	**0.00**	**0.00**

How many offspring is an individual expected to produce over its lifetime?

$$R_0 = \sum_{x=1}^{k} l_x m_x$$

For annual organisms we found that this quantity, R_0, which combines survival and fertility, is equal to fitness and completely determines how the frequency of genotypes/phenotypes changes over time through selection.

However, for organisms with age structure this simple quantity, R_0, does not completely describe fitness. If a stable age distribution has been reached, we can however, describe fitness using another relatively simple quantity:

$$r \approx \frac{\ln(R_0)}{\tau}$$

where τ is the generation time:

$$\tau = \frac{\sum_{x=1}^{k} l_x m_x x}{\sum_{x=1}^{k} l_x m_x}$$

Calculating r for the example shown above reveals an important point: In age structured populations that are growing, generation time is a fundamental component of fitness. Specifically, even though individuals of the two phenotypes produce, on average, identical numbers of offspring, the growth rate of z_2 is greater. Also, note the remarkable fact that once z_2

becomes fixed in the population, individuals die at younger ages ➔ the population has evolved early senescence, a fundamental shift in *life history*

Conclusion: In growing populations with age structure, natural selection favors phenotypes that increase r. Thus, NS favors phenotypes with effects on life histories that increase r, potentially favoring reductions in survival and/or fertility.

Conclusion not shown: Interestingly, in equilibrium populations, R_0 is a better measure of fitness. Thus, even the quantity that best measures fitness depends on ecology!

II. Predicting Evolutionary Change

We would like to predict how the phenotype distribution of the population will change over time. A reasonable starting point would be to predict the mean phenotype of the population in the next generation. How can we do this?

Key Assumptions:

- Annual organism
- Each parental individual characterized by a continuous phenotype z^p
- Each offspring individual characterized by a continuous phenotype z^o
- Each individual produces $W(z^p)$ offspring over its lifetime
- Population size, N, is sufficiently large for stochasticity to be ignored

i. The number of individuals in the next generation produced by individuals with phenotype z^p in the current generation is:

$$N'(z^p) = W(z^p)N(z^p)$$

ii. The total number of individuals in the next generation is:

$$N' = \int W(z^p)N(z^p)\,dz^p$$

iii. The frequency of individuals in the next generation that will be produced by individuals with phenotype z^p in the current generation is:

$$\phi'(z^p) = \frac{N'(z^p)}{N'} = \frac{W(z^p)N(z^p)}{\int W(z^p)N(z^p)\,dz^p} = \frac{N(z^p)}{N}\frac{W(z^p)}{\int \frac{N(z^p)}{N} W(z^p)dz^p}$$

$$= \phi(z^p)\frac{W(z^p)}{\int \phi(z^p)\,W(z^p)dz^p} = \phi(z^p)\frac{W(z^p)}{\bar{W}} = \phi(z^p)w(z^p)$$

iv. We can now use this information to calculate the mean phenotype in the next generation

$$\bar{z}' = \int z^o \phi(z^p) w(z^p) dz^p$$

v. However, we need to relate the phenotype of offspring to the phenotype of their parent. We will assume the following linear relationship:

$$z^o = \bar{z}^p + h^2(z^p - \bar{z}^p) + \varepsilon$$

vi. With this assumption the mean in the next generation is:

$$\bar{z}' = \int (\bar{z}^p + h^2(z^p - \bar{z}^p) + \varepsilon) w(z^p)\phi(z^p) dz^p$$

$$\bar{z}' = \int \left(\bar{z}^p w(z^p)\phi(z^p) + h^2 z^p w(z^p)\phi(z^p) - h^2 \bar{z}^p w(z^p)\phi(z^p) + \varepsilon\, w(z^p)\phi(z^p)\right) dz^p$$

$$= \bar{z}^p \bar{w}^p + h^2(\overline{z^p w^p} - \bar{z}^p \bar{w}^p)$$

$$= \bar{z}^p + h^2 Cov[z^p, w^p]$$

vii. And the change in the mean over a single generation is:

$$\Delta\bar{z} = \bar{z}' - \bar{z} = \bar{z}^p + h^2 Cov[z^p, w^p] - \bar{z}^p = h^2 Cov[z^p, w^p]$$

yielding our final result:

$$\Delta\bar{z} = h^2 Cov[z^p, w^p] \qquad (1)$$

or

$$\Delta\bar{z} = h^2 S \qquad (2)$$

or

$$\Delta\bar{z} = G\beta \qquad (3)$$

where:

$$S = Cov[z^p, w^p] = \bar{z}^{Selected} - \bar{z} \qquad (4)$$

$$\beta = \frac{Cov[z^p, w^p]}{V[z^p]} \qquad (5)$$

$$h^2 = \frac{G}{V[z^p]} \qquad (6)$$

Appendix 1. Notation

Symbol	Meaning
z^p	The phenotype of a parental individual
z^o	The phenotype of an offspring individual
$\bar{z}$	The population mean phenotype
N	The number of individuals in the population
$N(z)$	The number of individuals in the population with phenotype z
$\phi(z)$	The frequency of individuals in the population with phenotype z
$W(z)$	Absolute fitness. The number of offspring produced by an individual with phenotype z
$\bar{W}$	The average number of offspring produced by individuals within the population
$w(z)$	Relative fitness. The number of offspring produced by an individual with phenotype z relative to the average number produced by all individuals within the population
h^2	Heritability. The slope of the parent offspring regression. The proportion of phenotypic variation attributable to the additive action of genes