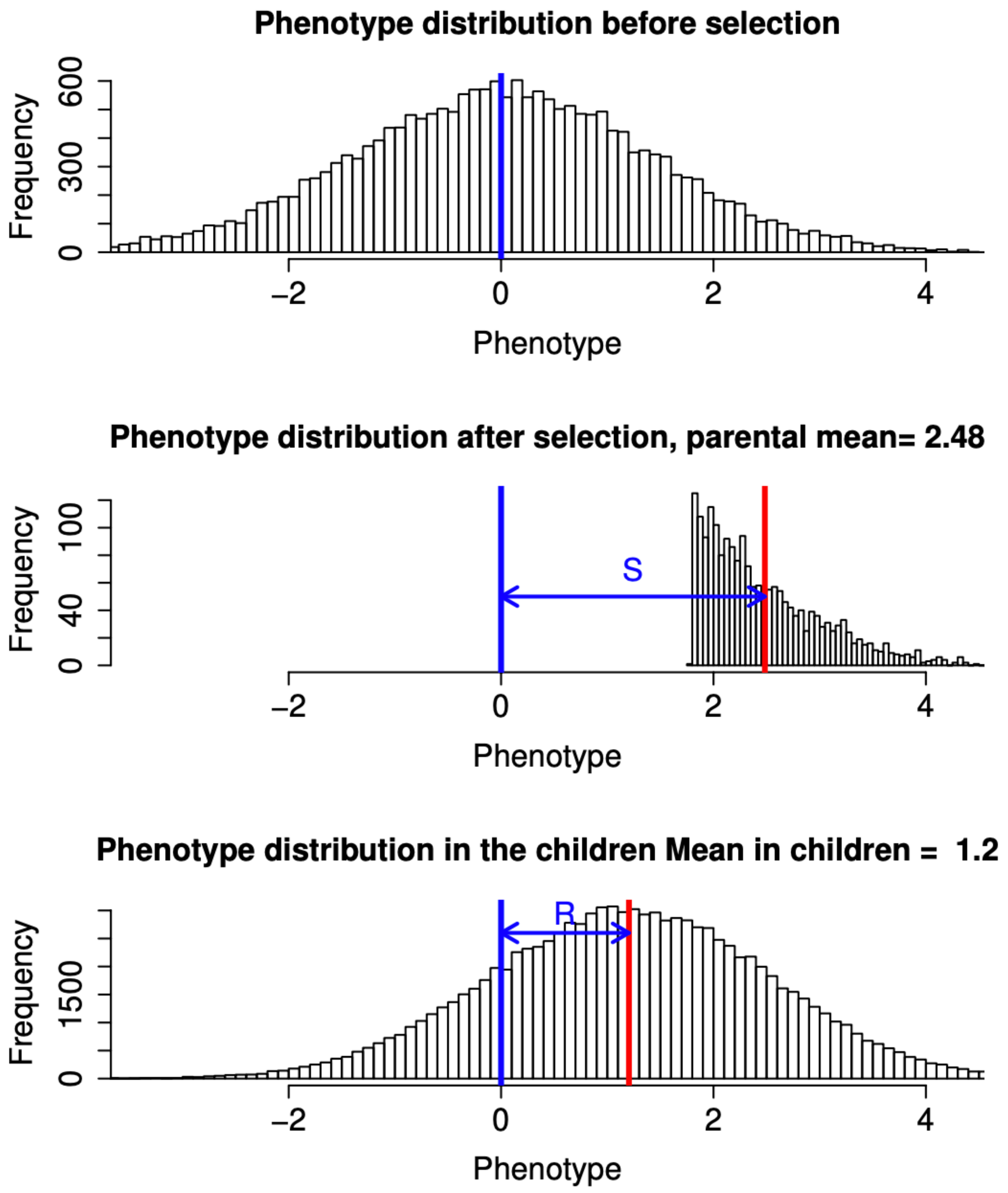
The Response to Phenotypic Selection

Evolution by natural selection requires

- Variation in a phenotype
- That survival and reproduction is non-random with respect to this phenotypic variation
- That this variation is heritable

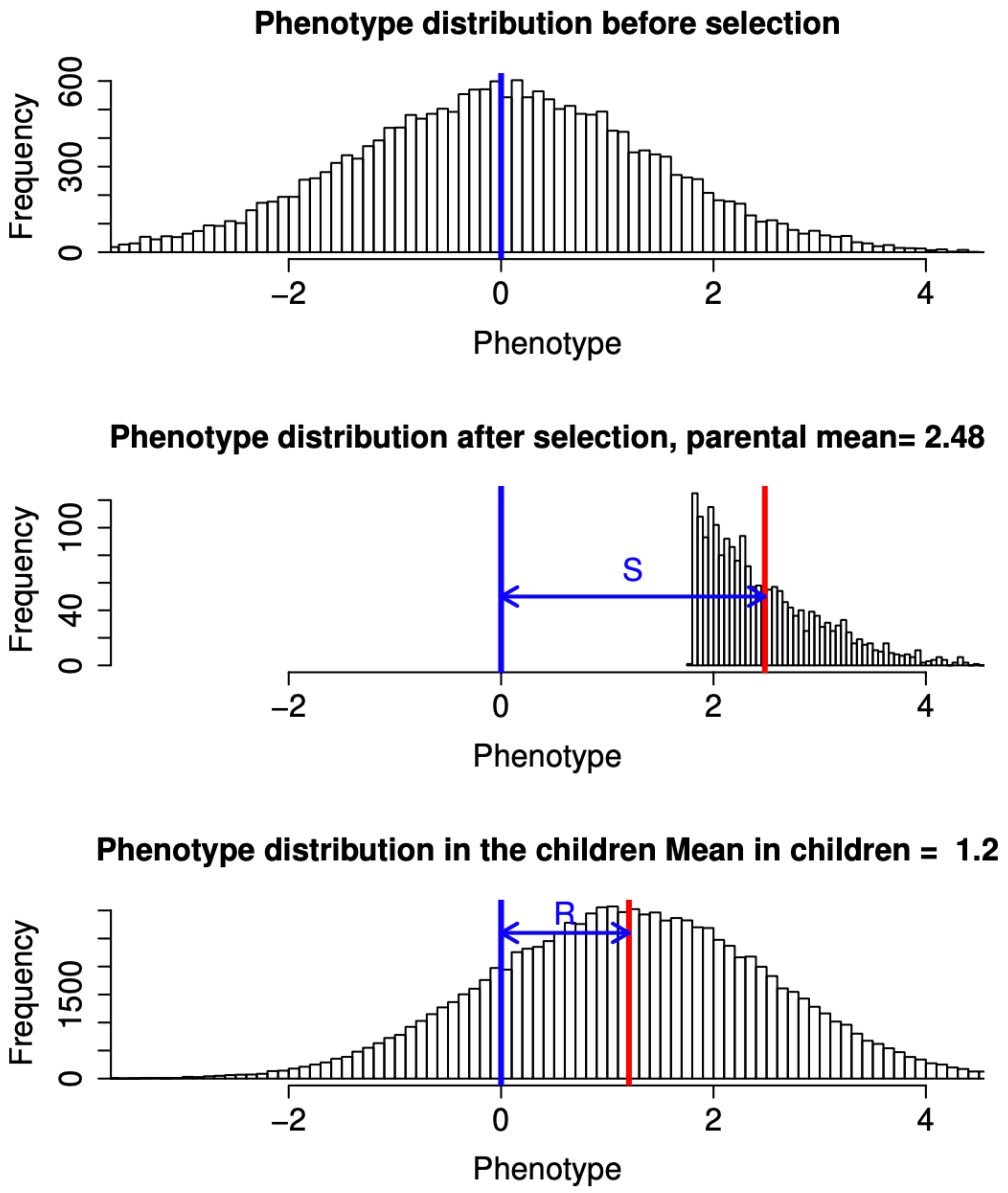
Response to selection



- μ_{BS}: pop mean before selection
- μ_S: pop mean after selection
- $S = \mu_S - \mu_{BS}$: selection differential
- What is the distribution of phenotypes in the next generation?
- $R = \mu_{NG} - \mu_{BS}$

Figure 8.1: **Top.** Distribution of a phenotype in the parental population prior to selection, $V_A = V_E = 1$. **Middle.** Only individuals in the top 10% of the phenotypic distribution are selected to reproduce; the resulting shift in the phenotypic mean is S. **Bottom.** Phenotypic distribution of children of the selected parents; the shift in the mean phenotype is R. Code here.

Response to selection



- The mean phenotype in the next generation is
- $$\mu_{NG} = \mathbb{E}\left(\mathbb{E}(X_{kid}|X_{mum}, X_{dad})\right)$$
- $$\mu_{NG} = \mu_{BS} + \beta_{mid,kid}(\mathbb{E}(X_{mid}) - \mu_{BS})$$
- $$\mathbb{E}(X_{kid}|X_{mum}, X_{dad}) = \mu + \beta_{mid,kid}(X_{mid} - \mu) = \mu + h^2(X_{mid} - \mu) \tag{7.16}$$
- $$\mu_{NG} = \mu_{BS} + h^2(\mu_S - \mu_{BS})$$
- $$R = \mu_{NG} - \mu_{BS} = h^2(\mu_S - \mu_{BS}) = h^2 S$$

Breeder's equation

- $R = h^2 S$
- Response to selection is proportional to selection differential, and narrow sense heritability

Estimate ‘realized’ h^2 from artificial selection

Question 1.

Galen (1996) explored selection on flower shape in *Polemonium viscosum*. She found that plants with larger corolla flare had more bumblebee visits, which resulted in higher seed set and a 17% increase in corolla flare in the plants contributing to the next generation. Based on the data in the caption of Figure 8.3 what is the expected response in the next generation?

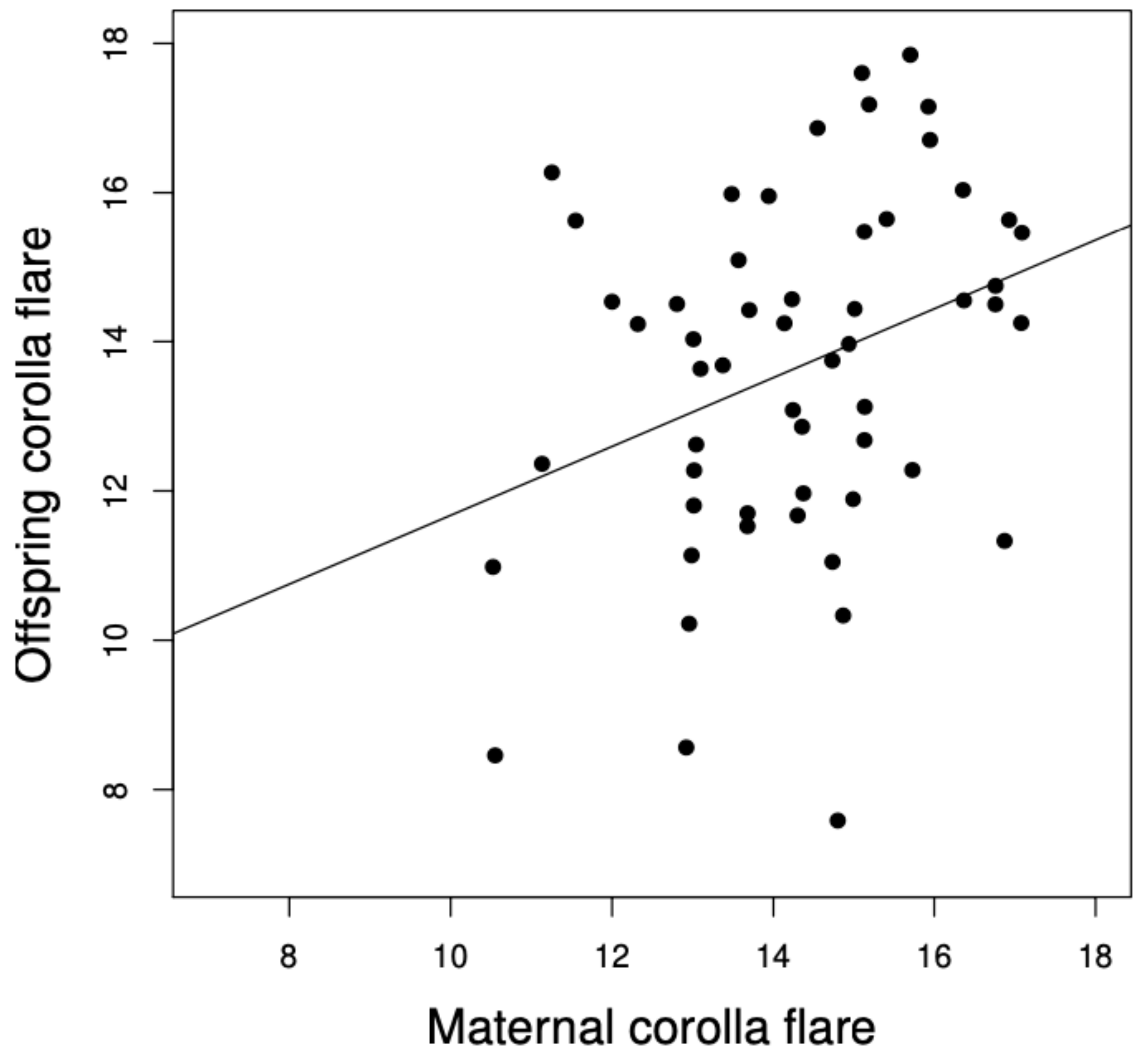


Figure 8.3: The relationship between maternal and offspring corolla flare (flower width) in *P. viscosum*. From Galen’s data the covariance of mother and child is 1.3, while the variance of the mother is 2.8. Data from Galen (1996). Code here.

Estimate ‘realized’ h^2 from artificial selection

Question 2.

From the experiment shown in Figure 8.5, the mean corn oil content in 1897 was 4.78, among the 24 individuals chosen to breed to for the next generation the mean was 5.2. The offspring of these individuals had a mean kernel oil content of 5.1. What is the narrow sense realized heritability?

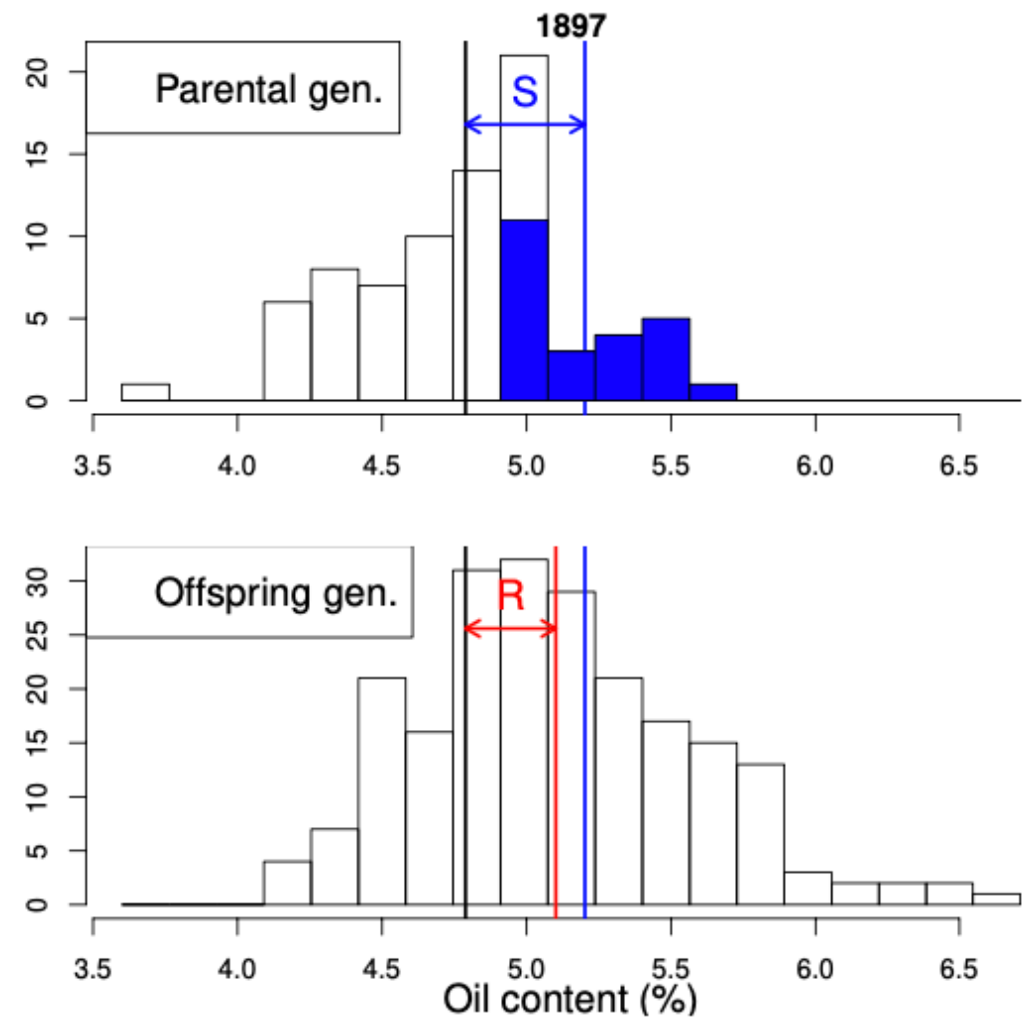


Figure 8.5: **Top.** Phenotypic distribution of oil in corn in 1897, and the individuals who were selected to breed for the next generation are marked in blue. **Bottom.** The distribution in the next generation. Data from the Illinois selection experiment available here, Code here.

Genetic basis of the response to selection

- Average individual before selection carried 100 of these 'up' alleles
- Average individual surviving selection carries 108 'up' alleles
- Average child of the selected parents carries 108 up alleles
- Average frequency of an 'up' allele has changed from 50% to 54%

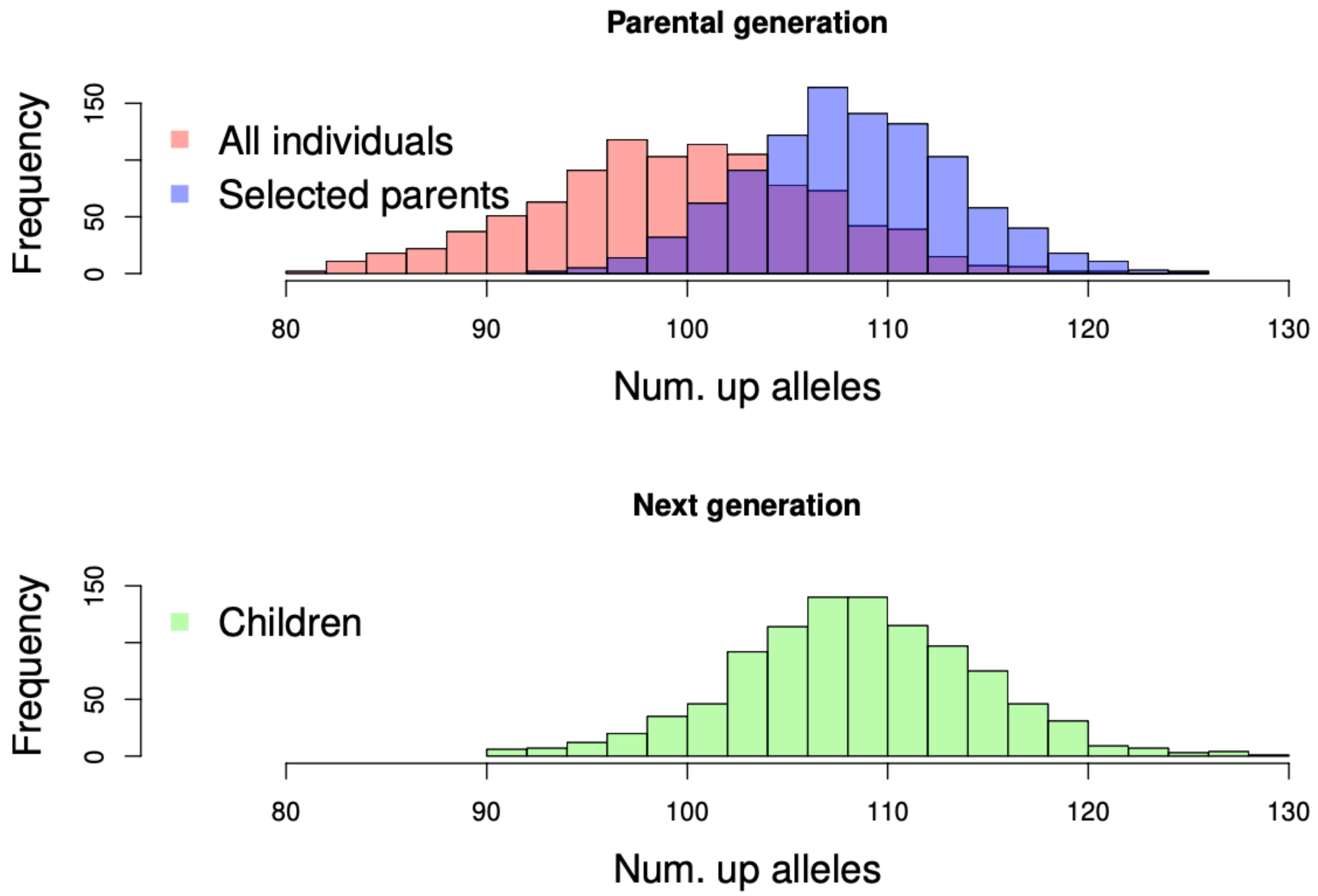


Figure 8.6: **Top.** Distribution of the number of up alleles in the parental population prior to selection (red), for the selected individuals in the top 10% phenotypic tail of the population (blue) **Bottom.** The same distribution for the offspring of the selected parents in the next generation (green). Code here.

Long term response to selection

- Long term response to selection
  - $R_n = nh^2S$
- Field experiment in Illinois
- Plant breeders have systematically selected for higher and lower oil content in corn for or over a century.
- Seeds from the plants in the extremes of the distribution used to form the next generation
- Up-selection line went from a mean oil content of 4.7% in 1896 to 22.1% in 2004

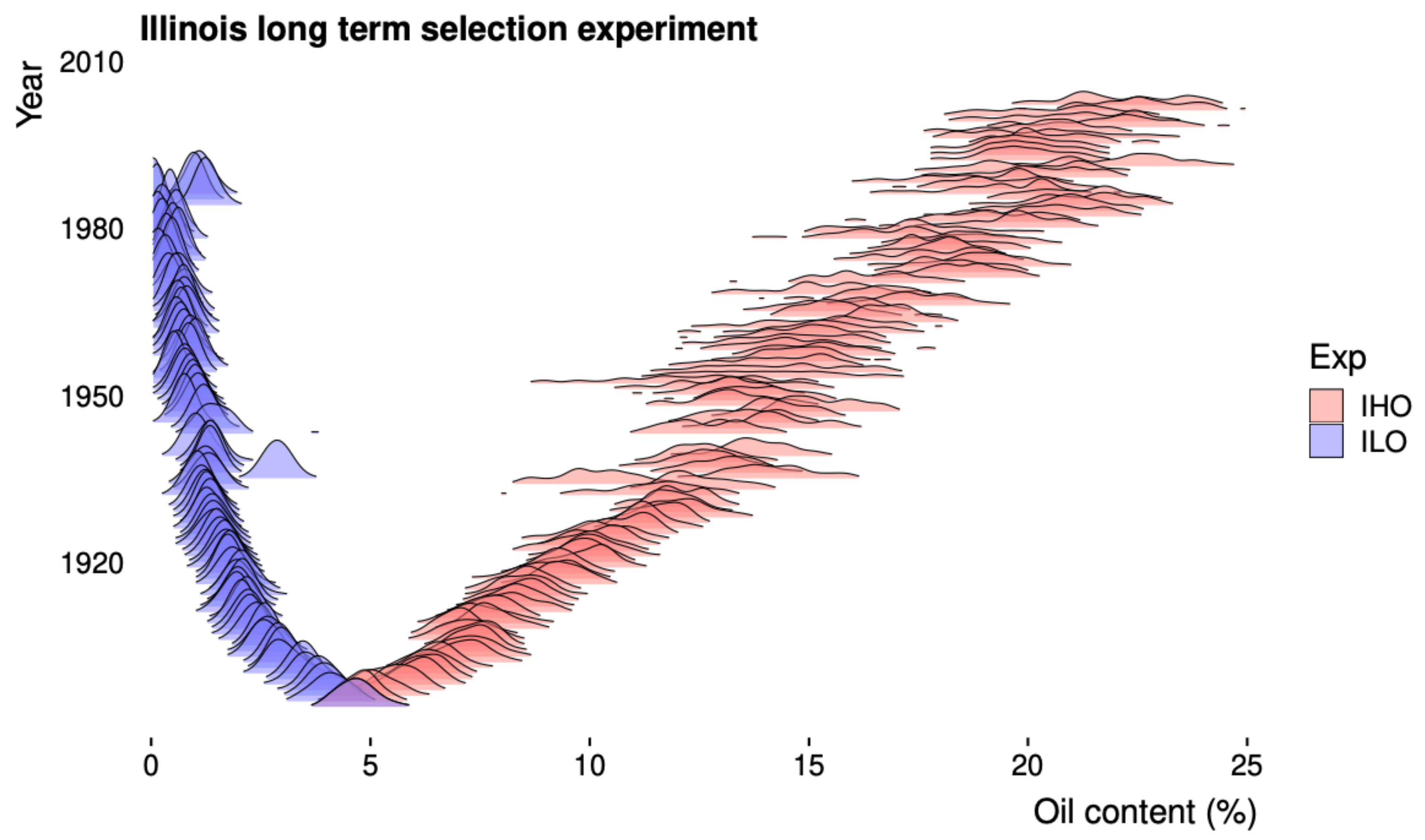


Figure 8.8: Density plots showing the phenotypic distributions of the up- and down-selection populations of the Illinois long term selection experiment over time. Data available here, Code here.

Directional selection as the covariance between fitness and phenotype

- mean phenotype before selection is
- $$\mu_{BS} = \mathbb{E}[X] = \int_{-\infty}^{\infty} xp(x)dx \qquad (8.7)$$
- Distribution of phenotypes in those surviving to reproduce is
- $$\mathbb{P}(X|\text{survive}) = \frac{p(x)w(x)}{\int_{-\infty}^{\infty} p(x)w(x)dx}. \qquad (8.8)$$
- mean fitness of the population
- $$\overline{w} = \int_{-\infty}^{\infty} p(x)w(x)dx. \qquad (8.9)$$

- Mean phenotype of inds surviving to reproduction
  - $$\mu_S = \frac{1}{\overline{w}} \int_{-\infty}^{\infty} x p(x) w(x) dx \qquad (8.10)$$
- mean center the distribution of phenotypes, selection differential
  - $$S = \mu_S = \frac{1}{\overline{w}} \int_{-\infty}^{\infty} x p(x) w(x) dx = \frac{1}{\overline{w}} \mathbb{E}\left(X w(X)\right) \qquad (8.11)$$
  - $$S = \mathbb{E}\left(X^{w(X)}/\overline{w}\right) = Cov\left(X, {}^{w(X)}/\overline{w}\right) \qquad (8.12)$$
  - $$R = \frac{V_A}{V_P} Cov\left(X, {}^{w(X)}/\overline{w}\right) \qquad (8.13)$$

Fitness Gradients and linear regressions

- linear regression of an mean-centered phenotype (X_i) on fitness (W_i)
- $$W_i \sim \beta X_i + \overline{w} \qquad (8.14)$$
- $$\beta = Cov(X, {}^{w(X)}/_{\overline{w}})/V_P \qquad (8.15)$$
- $$R = V_A \beta \qquad (8.16)$$
- Directional response to selection if there is a linear relationship of phenotype on fitness, and if there is additive genetic variance for the phenotype

Fisher's fundamental theorem of natural selection

- choose relative fitness to be our phenotype ($X = w(X)/\overline{w}$)

- $$\begin{aligned} R &= \frac{V_A}{V_P} Cov\left(w(X)/\overline{w}, w(X)/\overline{w}\right) = \frac{V_A}{V_P} V_P \\ &= V_A \end{aligned} \tag{8.17}$$

- "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time." -Fisher (1930) (pg 37)

Directional Selection on Fitness Landscapes

- $$R = \frac{V_A}{\overline{w}} \frac{\partial \overline{w}}{\partial \bar{x}}$$

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- $$\begin{aligned} \frac{1}{\overline{w}} \frac{\partial \overline{w}}{\partial \bar{x}} &= \frac{1}{\overline{w}} \int_{-\infty}^{\infty} w(x) \frac{\partial p(x)}{\partial \bar{x}} dx \\ &= \int_{-\infty}^{\infty} \frac{w(x)}{\overline{w}} \frac{(x - \bar{x})}{V_P} dx \\ &= \frac{cov(w(x), x)}{var(x)} \qquad (8.18) \end{aligned}$$

- $\overline{w} = \int w(x)\, p(x)\, dx$
- $\dfrac{\partial \overline{w}}{\partial \overline{x}} = \dfrac{\partial}{\partial \overline{x}} \int w(x)\, p(x; \overline{x})\, dx$
- $= \int w(x)\, \dfrac{\partial p(x; \overline{x})}{\partial \overline{x}}\, dx$

- Assume Normal Distribution for Trait
- $p(x; \overline{x}) = \dfrac{1}{\sqrt{2\pi V_P}} \exp\left(-\dfrac{(x - \overline{x})^2}{2V_P}\right)$
- $\dfrac{\partial p(x; \overline{x})}{\partial \overline{x}} = p(x; \overline{x}) \cdot \left(\dfrac{x - \overline{x}}{V_P}\right)$

- $$\frac{\partial \overline{w}}{\partial \overline{x}} = \int w(x) \cdot p(x; \overline{x}) \cdot \left(\frac{x - \overline{x}}{V_P} \right) dx$$

- $$= \frac{1}{V_P} \int (x - \overline{x}) w(x) p(x; \overline{x})\, dx$$

- $$= \frac{1}{V_P} \cdot \mathrm{Cov}(x, w)$$

- Finally,
  - $$\frac{\partial \overline{w}}{\partial \overline{x}} = \frac{1}{V_P} \cdot \mathrm{Cov}(x, w)$$

$$R = V_A \cdot \frac{\partial \ln \overline{w}}{\partial \overline{x}}$$