

Quantitative characters III: response to selection in nature

Selection occurs whenever there is a nonrandom relationship between phenotypes (performances) and fitnesses.

But *evolution* occurs only when there is heritable (additive) variation for the phenotypes.

The *rate* of evolutionary change depends on the *strength* of selection and the *amount* of additive genetic variation.

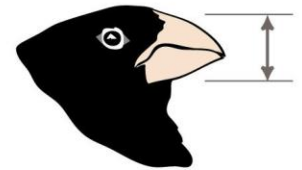
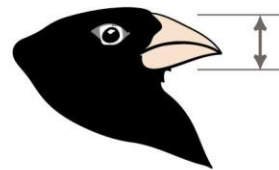
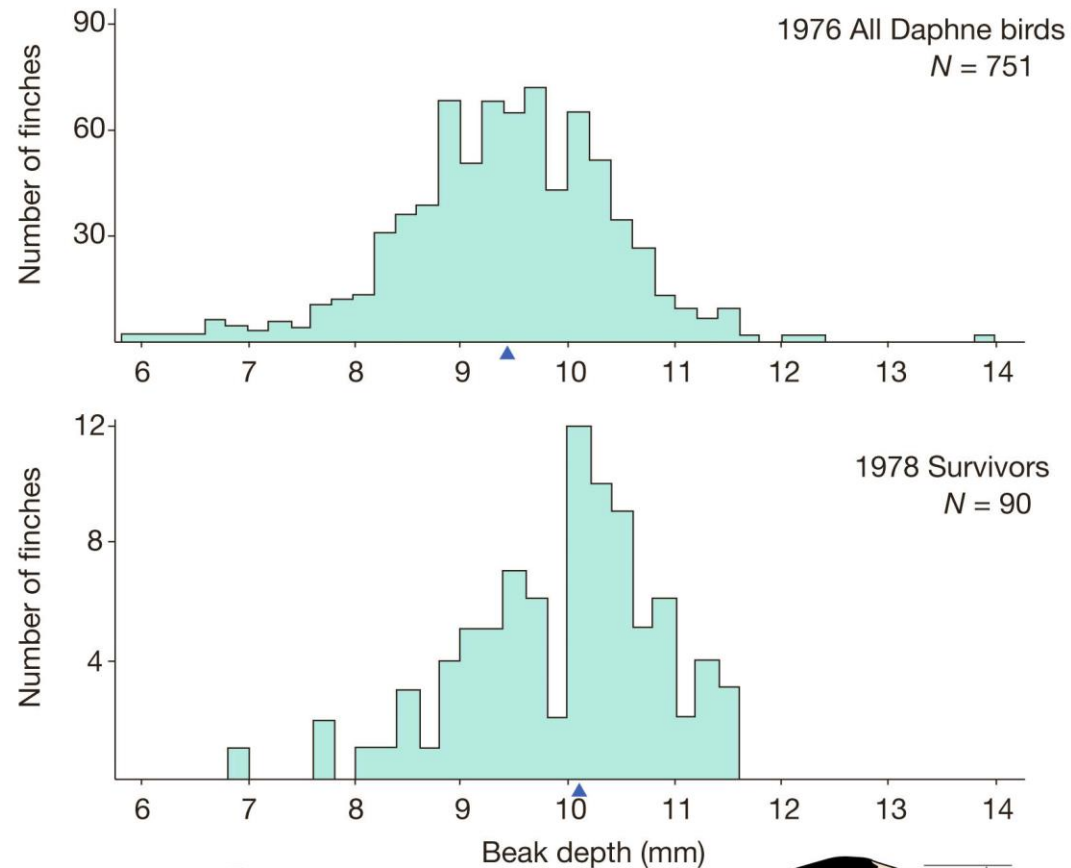
For directional selection, there are two equivalent ways to represent this relationship:

$$R = h^2 S$$

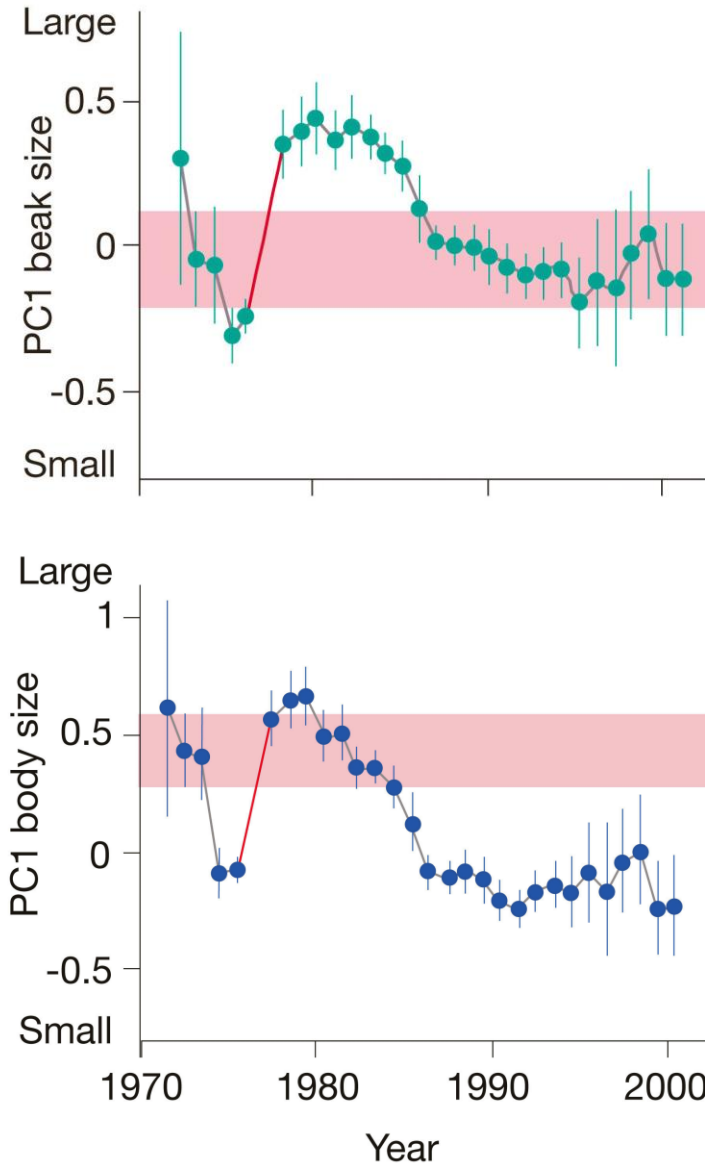
(response = heritability x selection differential)

$$\Delta x = V_A \beta$$

(change = additive variance x selection gradient)



Some quantitative traits have been observed to evolve very rapidly. For example: beak and body sizes of *Geospiza fortis* on Isla Daphne Major



Beak size and body size increase dramatically in response to the drought of 1977, but both then decrease slowly.

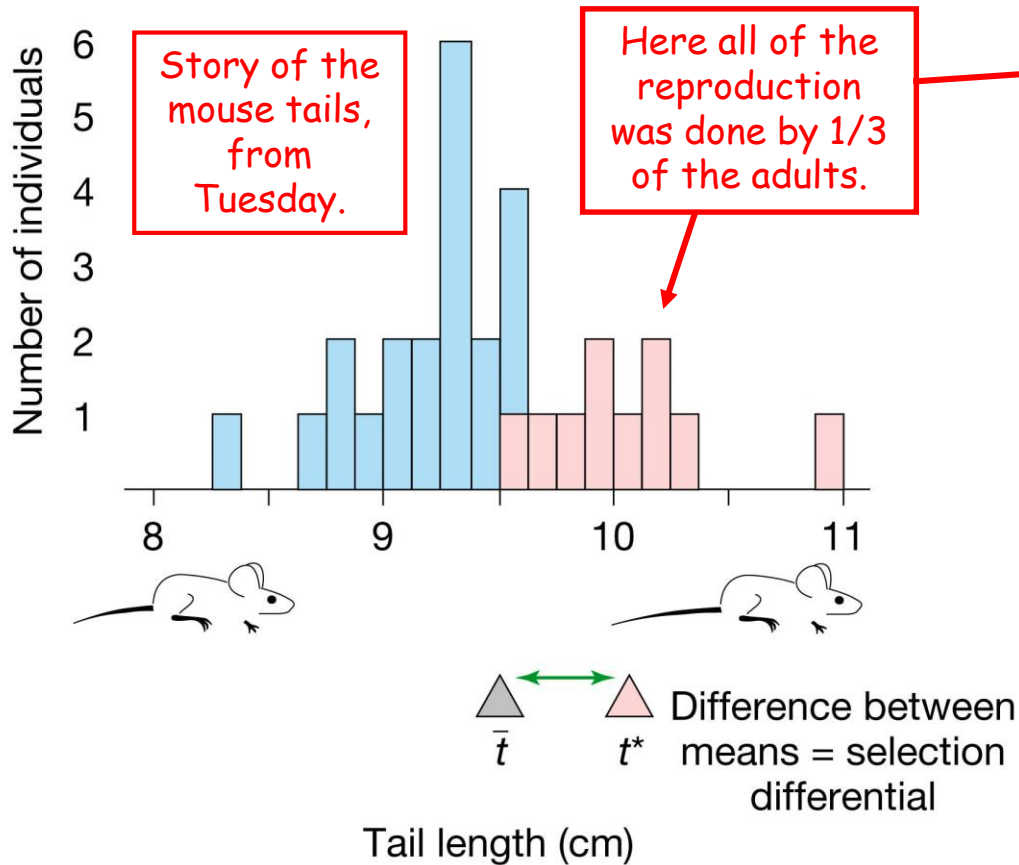
Adaptation to a tradeoff:
Larger beaks and bodies are favored when most seeds are large and hard;
smaller beaks and bodies are favored when most seeds are small and soft.

S and β quantify the strength of selection

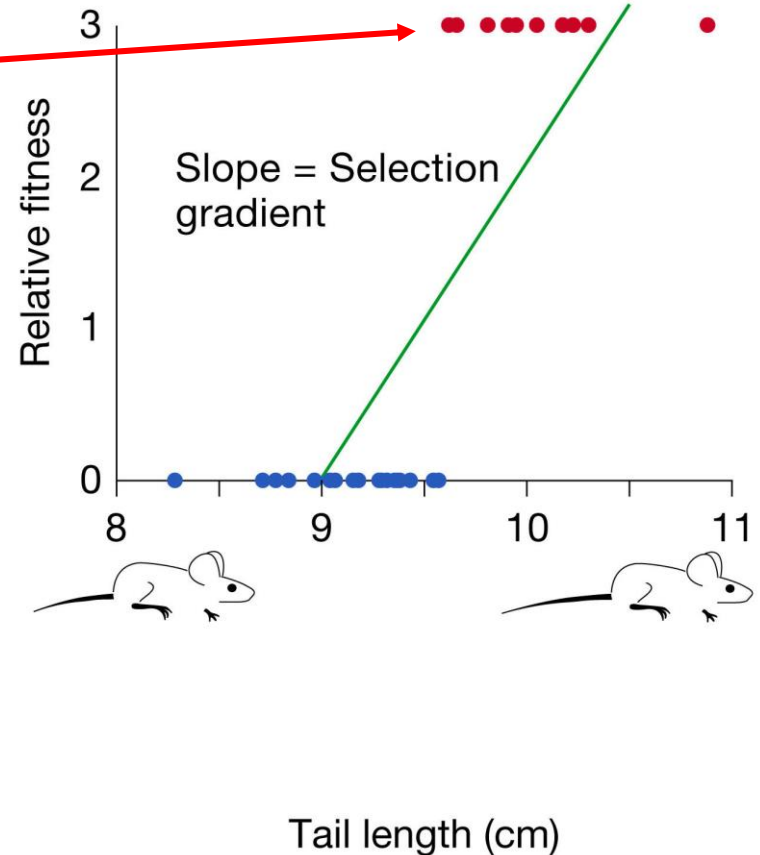
S (the selection differential) is the difference between the mean phenotype of the reproductively successful parents and the whole population (of potential parents).

B (the selection gradient) is the slope of the regression describing the relationship between fitness (y) and values of the phenotype (x), when mean fitness is normalized to 1.

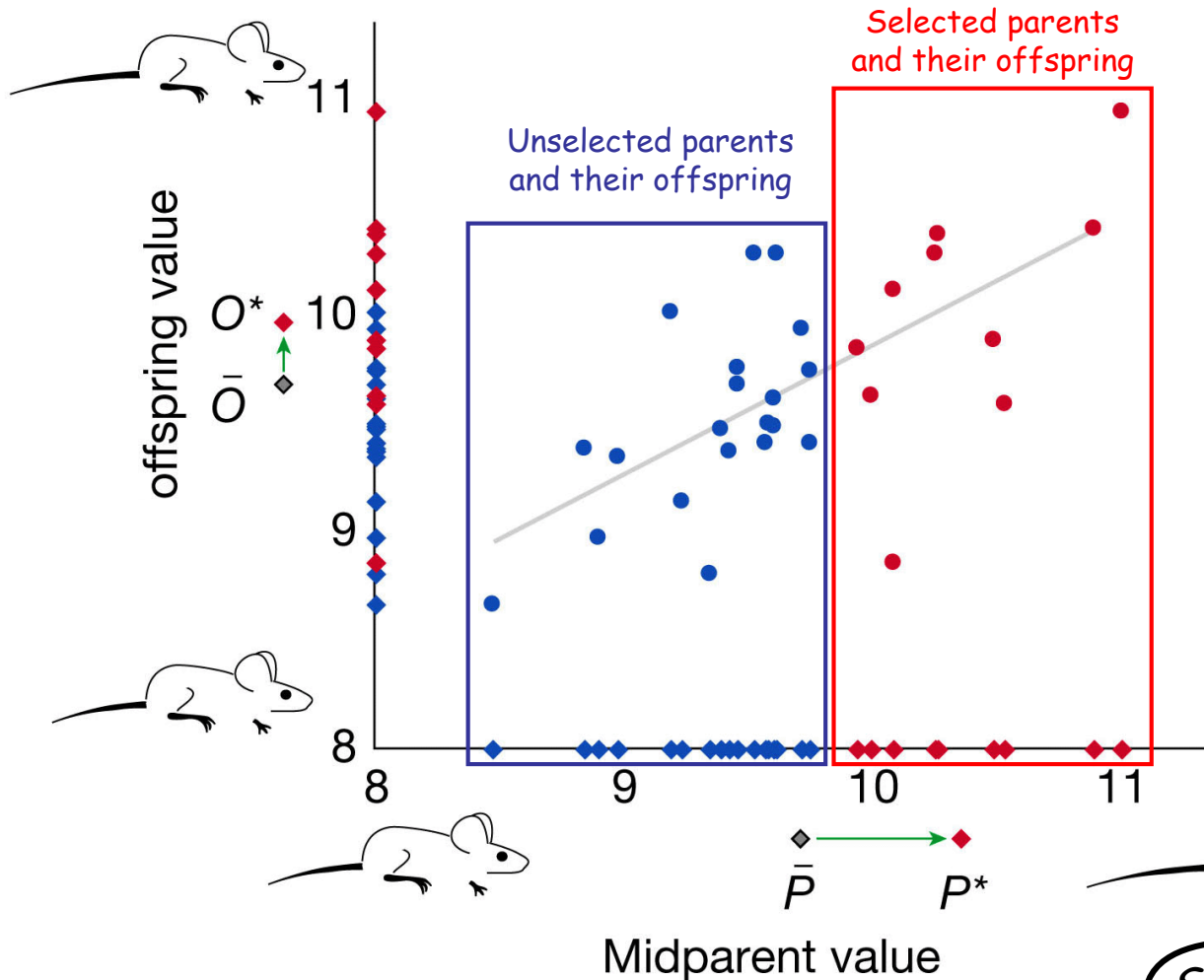
The selection differential



The selection gradient



This "geometric" interpretation of heritability shows why $R = h^2S$
 $(h^2 = R/S)$



R = response to selection
 S = selection differential

$$\text{Slope} = h^2 = \frac{[O^* - \bar{O}]}{[P^* - \bar{P}]} = \frac{R}{S}$$

$$R = h^2S$$

And $h^2 = V_A/V_P$,
 so $R = (V_A/V_P)S$.

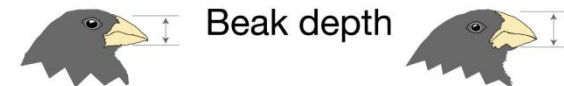
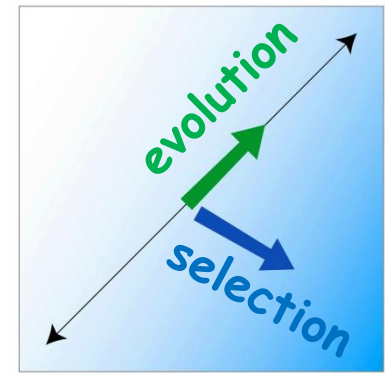
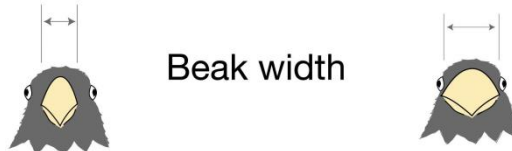
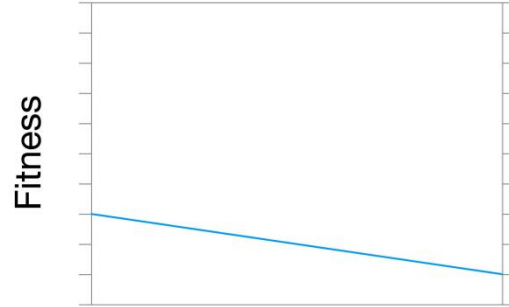
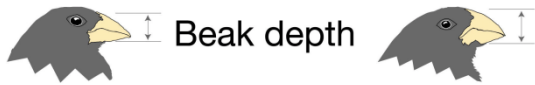
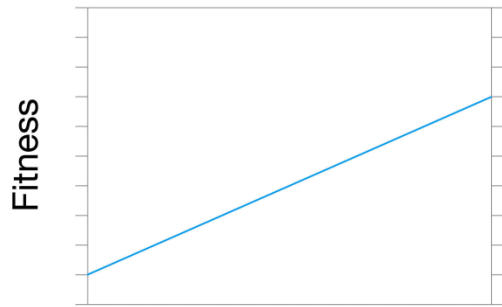
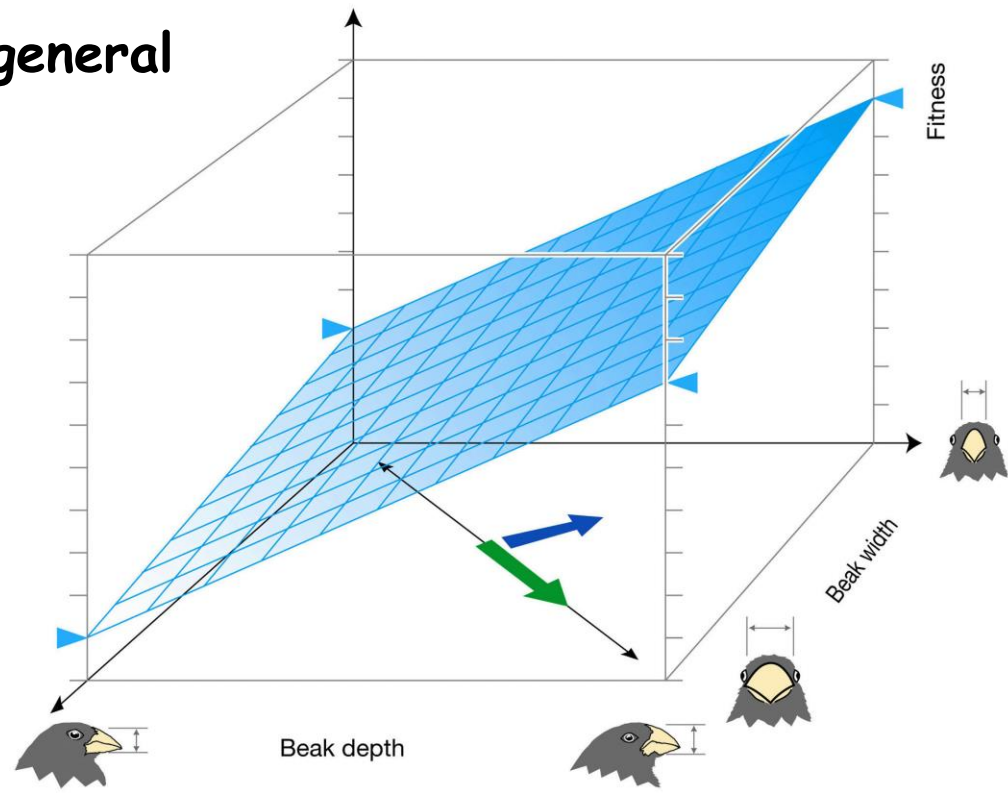
And S/V_P is equivalent to β ,
 so $\Delta x = V_A \beta$

So you see, the evolutionary response to selection is proportional to the additive genetic variance! Squeak!

The selection gradient is more general

It accommodates messy, *continuous* relationships between phenotypes and fitnesses.

And it allows us to predict what will happen when two or more quantitative traits are *correlated* with each other owing to genetic or developmental constraints.

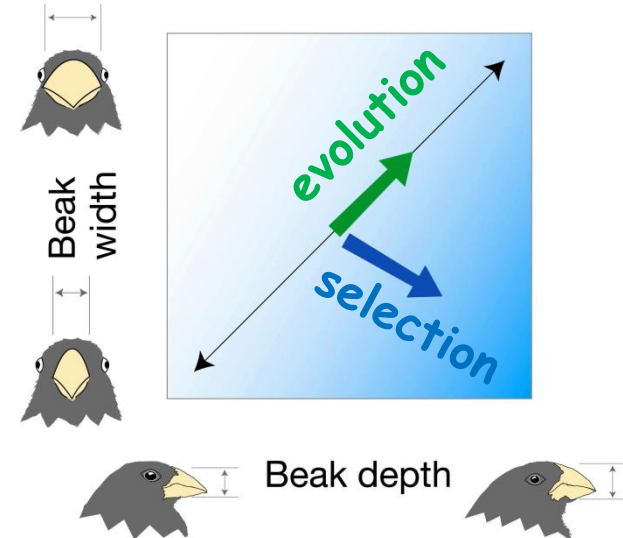
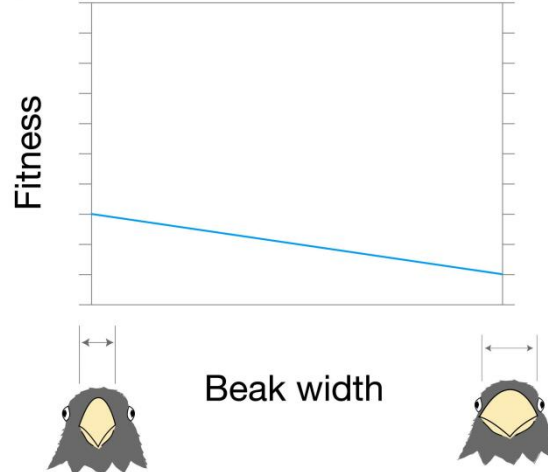
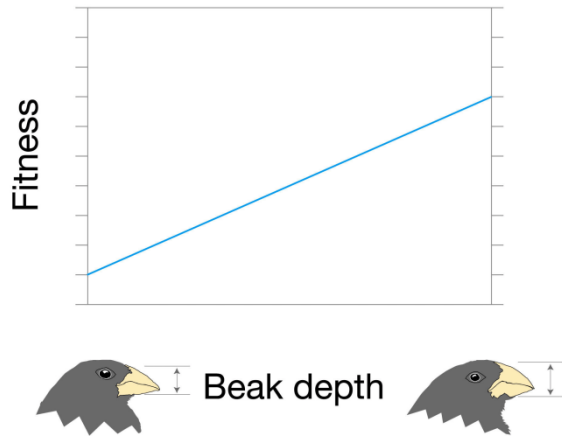
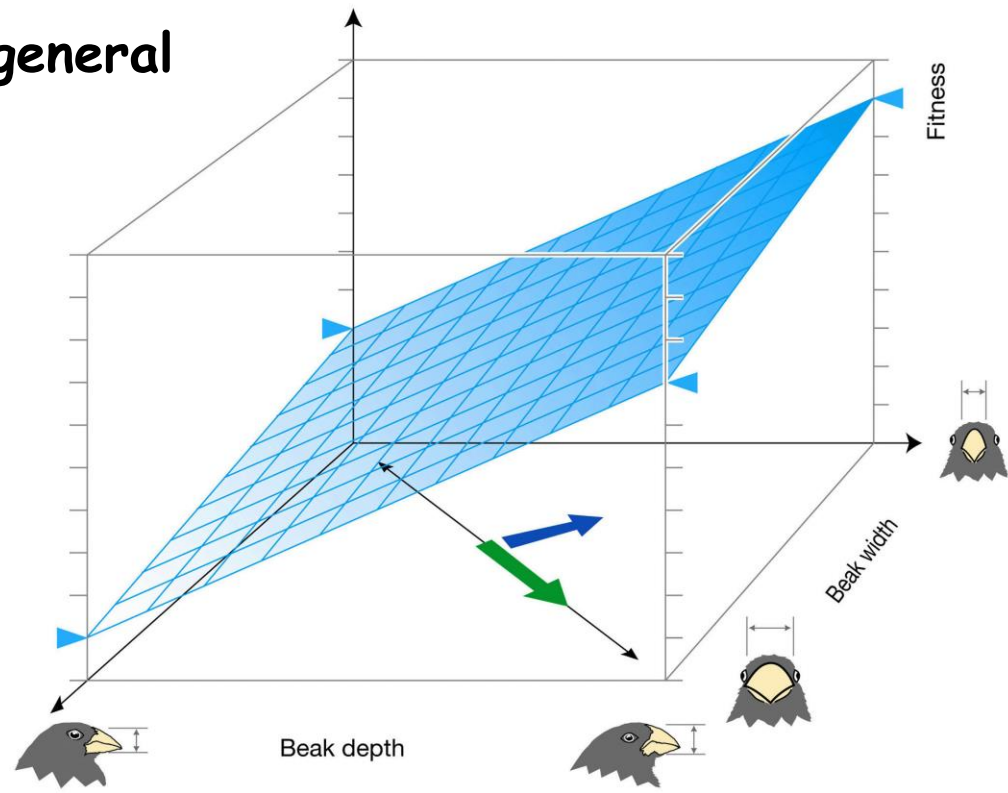


The selection gradient is more general

It accommodates messy, *continuous* relationships between phenotypes and fitnesses.

For more about the nuts and bolts of this approach, see Alan's short essay (*Response to Natural Selection on a Quantitative Character*), which is posted in the Lectures section of the course web site.

<https://content.csbs.utah.edu/~rogers/tch/an+5221/unprotected/Rogers-lande.pdf>



An application: bumblebees select on flower size in alpine skypilots

Candace Galen noticed that alpine skypilots (*Polemonium viscosum*) growing at high (tundra) elevations on Pennsylvania Mountain in the Colorado Rockies have flowers that are 12% larger than those growing at lower (timberline) elevations.



At timberline, skypilots are pollinated by a variety of insects including flies, small solitary bees, and bumblebees. But higher in the tundra, the only pollinators are bumblebees.

Plants with larger flowers attract more bumblebees, and flowers that attract more bees set more seeds.

Did the tundra populations evolve larger flowers *because* bumblebees (their only pollinators) prefer large flowers?

Galen first estimated the heritability of flower size ("corolla flare").

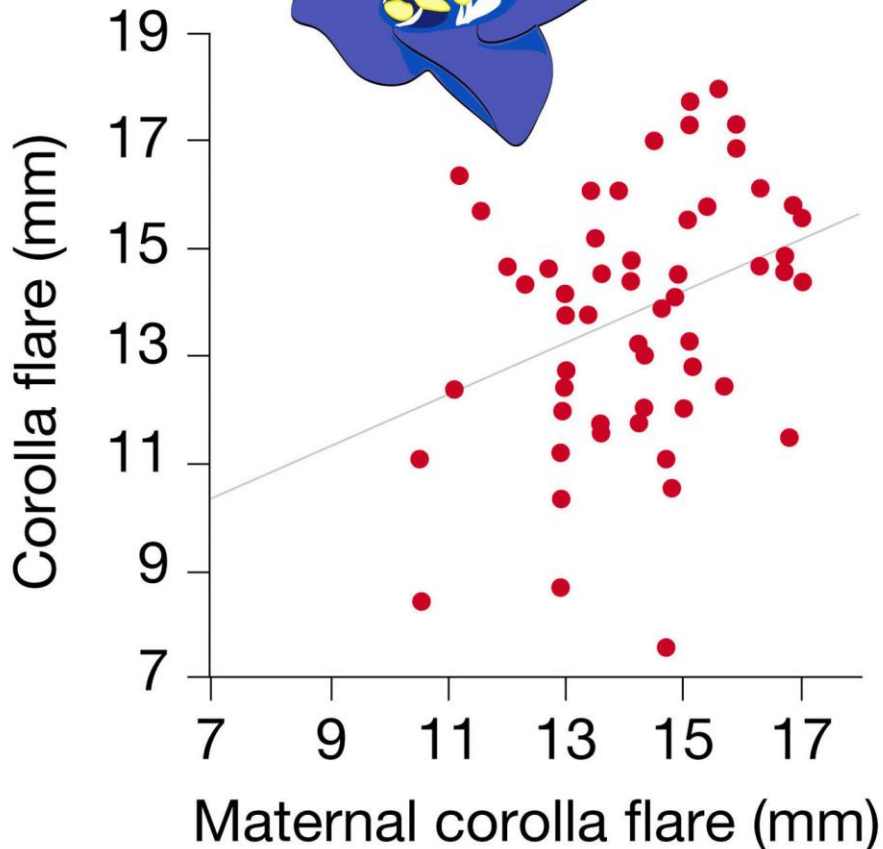
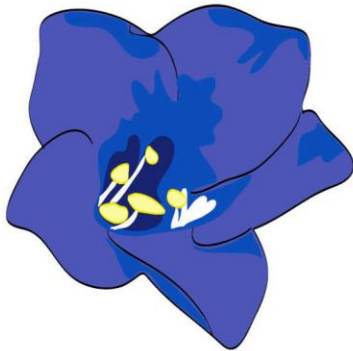
Then she caged a large number of plants with bumblebees, allowed them to set seeds, germinated the seeds, and then planted the seedlings at random locations in their natural habitat.

Six years later she counted the survivors.



The heritability of corolla flare was roughly $h^2 = 0.5$.

$$V_A = h^2 V_P = 0.5 * 5.66 = 2.83$$

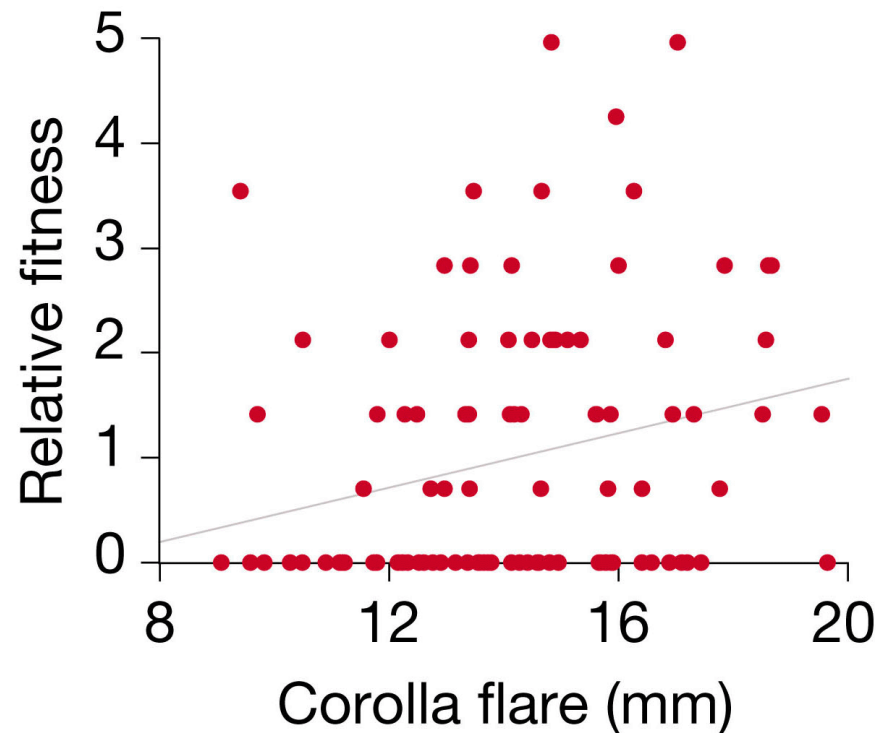


The selection gradient caused by bumblebee pollination was $\beta = 0.13$ (average relative fitness increased 13% per millimeter of corolla flare).

Predicted response:

$$\Delta x = V_A \beta \approx 2.83 * 0.13 \approx 0.37 \text{ mm/generation}$$

This is 2.6% per generation. Thus a 12% increase could evolve in just 5 generations!



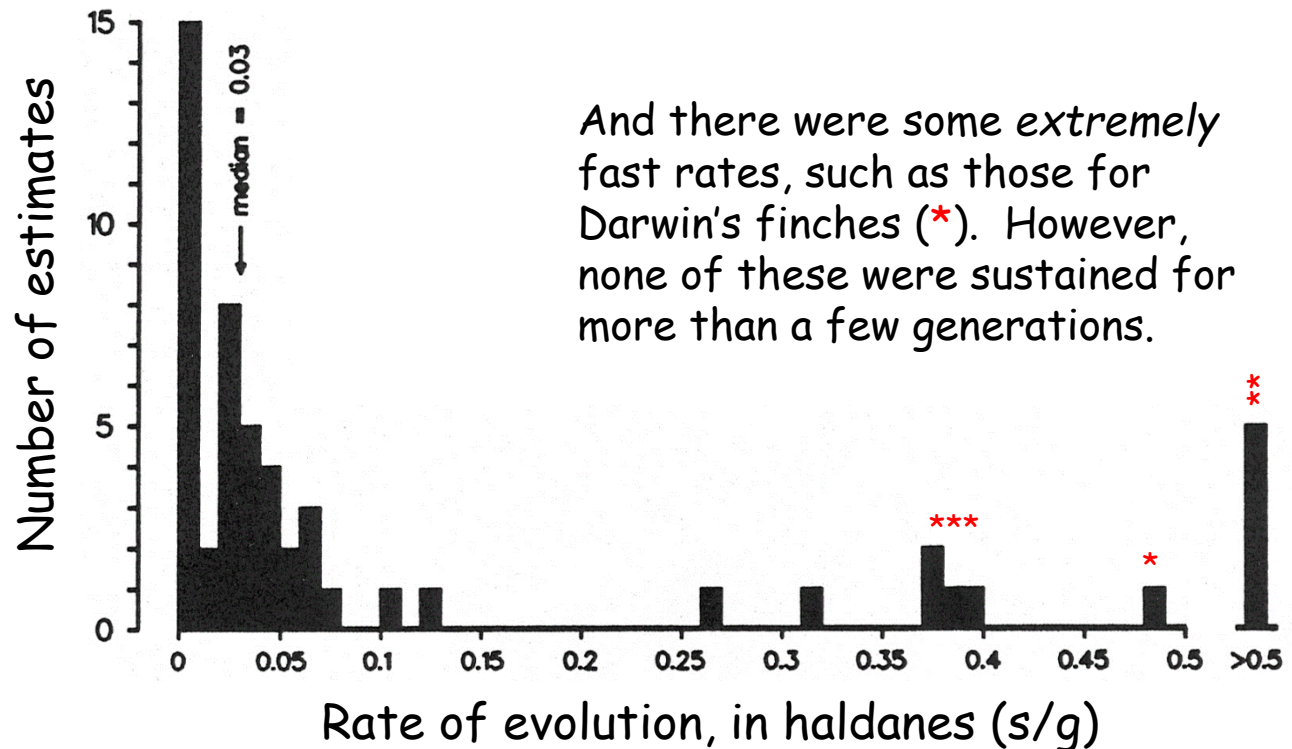
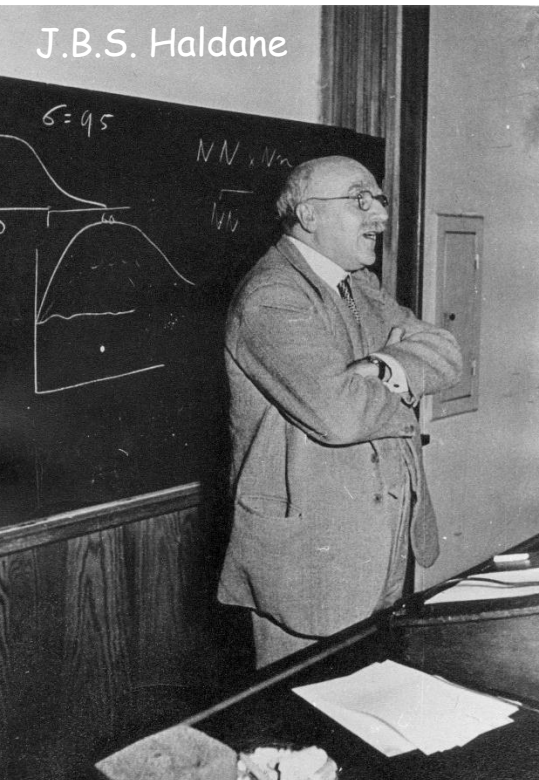
How fast do quantitative traits evolve (today) in nature?

Hendry and Kinnison (1999) reviewed 54 rates of phenotypic evolution that had been estimated in 20 different studies of fish, birds, mammals, lizards and bugs.

They converted all of the estimated rates of phenotypic change to units of *phenotypic standard deviations per generation* (called "haldanes" because J.B.S. Haldane appears to have been the first person to suggest this standardization).

The median rate of evolution was 0.03 haldanes (3% of a s.d. per generation).

At that rate the mean would move **3** standard deviations in only 100 generations!



How fast do they evolve over evolutionary time?

A different scale of measurement is used in most paleontological studies.

Darwins = proportional trait-value change in units of e per million years

$$[\log(x_1) - \log(x_2)]/T_{\text{myr}}$$

	Number	Time interval	Rate (Darwins)
Selection experiments	8	3.7 yr	58700
Recent colonizations	104	170 yr	370
Post-Pleistocene mammals	46	8200 yr	3.7
Fossil vertebrates	228	1.6 MY	0.08
Fossil invertebrates	135	7.9 MY	0.07

Table 6.5: Rates of morphological evolution. The time intervals are measured in either years (yr) or millions of years (MY). The table is from Maynard Smith (1989).

Kinnison & Hendry (2001) reviewed current microevolutionary rates for over 2000 traits from 47 studies of 30 species.

The median rate, in darwins, was 1150 (3-4 orders of magnitude greater than long-term rates of evolution as seen in the fossil record). In haldanes, the median rate was 0.005 (somewhat smaller than in their 1999 review).

Still, the upshot is that quantitative traits evolve *remarkably rapidly* (in the short term), but the direction of evolution reverses course so often that little change occurs (on average) over the long term.

Will most species show human-like genomic evidence of rapid recent adaptation? Selective sweeps, etc.? Stay tuned!

In natural populations, heritable variation is abundant but maleable.

Clausen, Keck & Heisey grew the same genotypes of *Achillea* at different elevations in California.

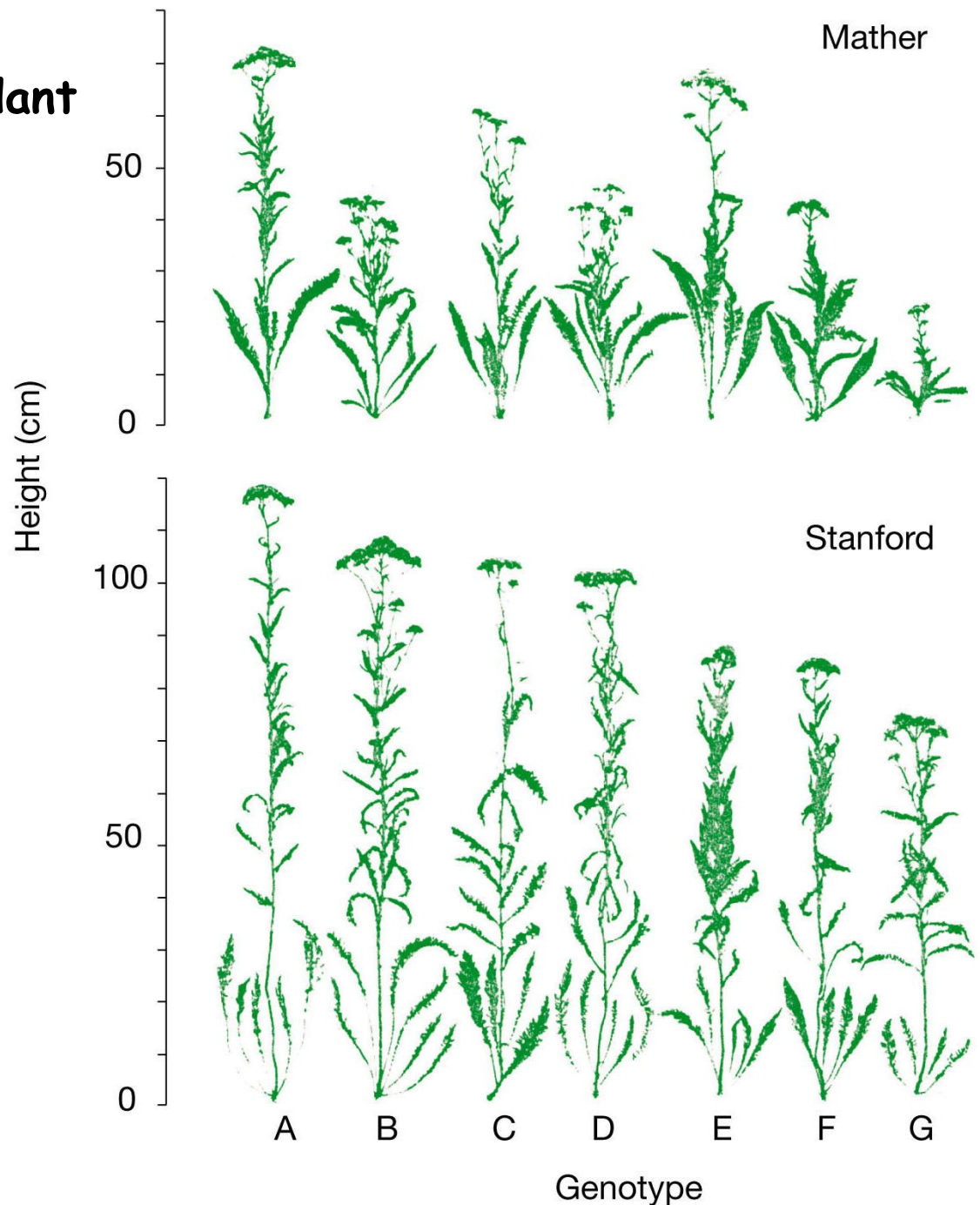
Plant height was highly variable and heritable in each environment, and *all* genotypes were shorter at high elevation (Mather).

However, some plants that were relatively tall in one environment were relatively short in the other.

Thus the *genetic* variance depends on the population's environment!

And the *environmental* variance depends on the population's genes!

This situation-dependence of the variance components is called "*genotype by environment (G x E) interaction*".



How genetic variation is created and destroyed by the environment!

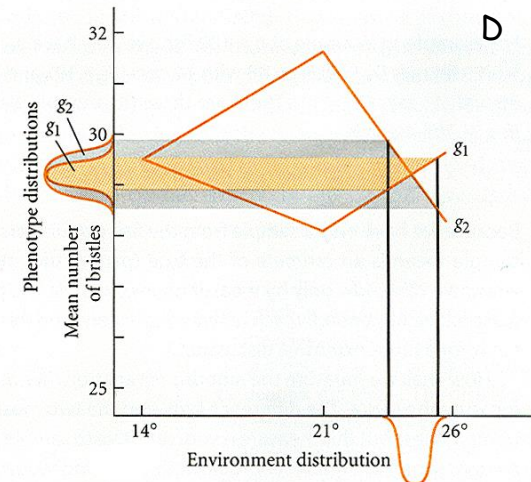
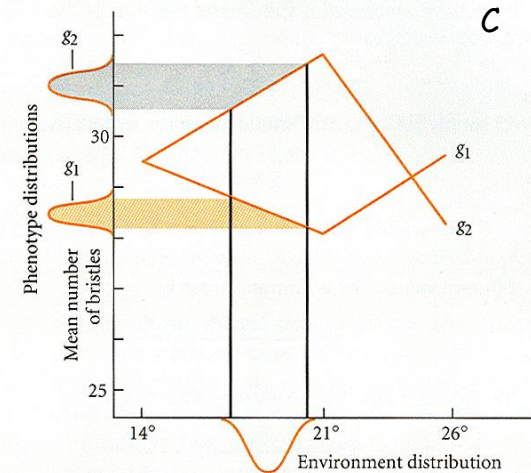
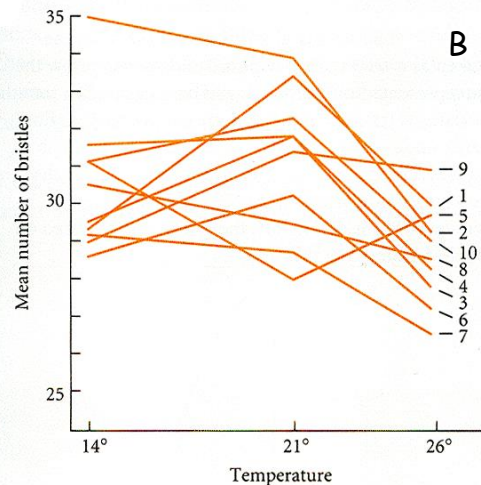
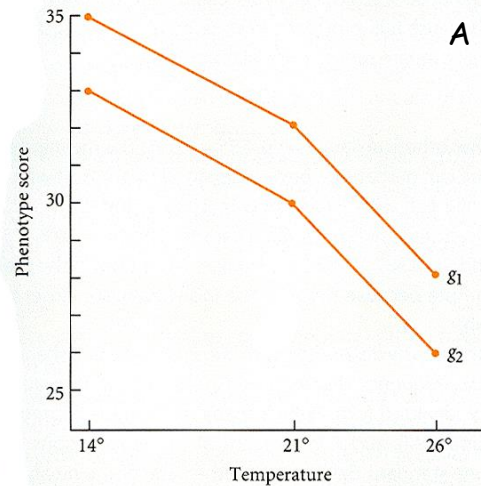
The "norm of reaction" is a graph describing how a given genotype responds to different states of the environment.

A Two hypothetical genotypes that produce different phenotypes at different temperatures, but always with the same difference between them. No GxE interaction.

B Real norms of reaction for bristle number in 10 *Drosophila* genotypes raised at different temperatures. Much GxE.

C Distributions of bristle number expected for a population containing two of these genotypes, when raised at low to middling temperatures. Considerable additive genetic variation and *high heritability* of bristle number.

D The same population raised at a higher average temperature, where the norms of reaction cross. No additive genetic variation and *no heritability*!



Upshot: the heritability of a trait can be defined only for a *given population (gene pool) in a given environment.*

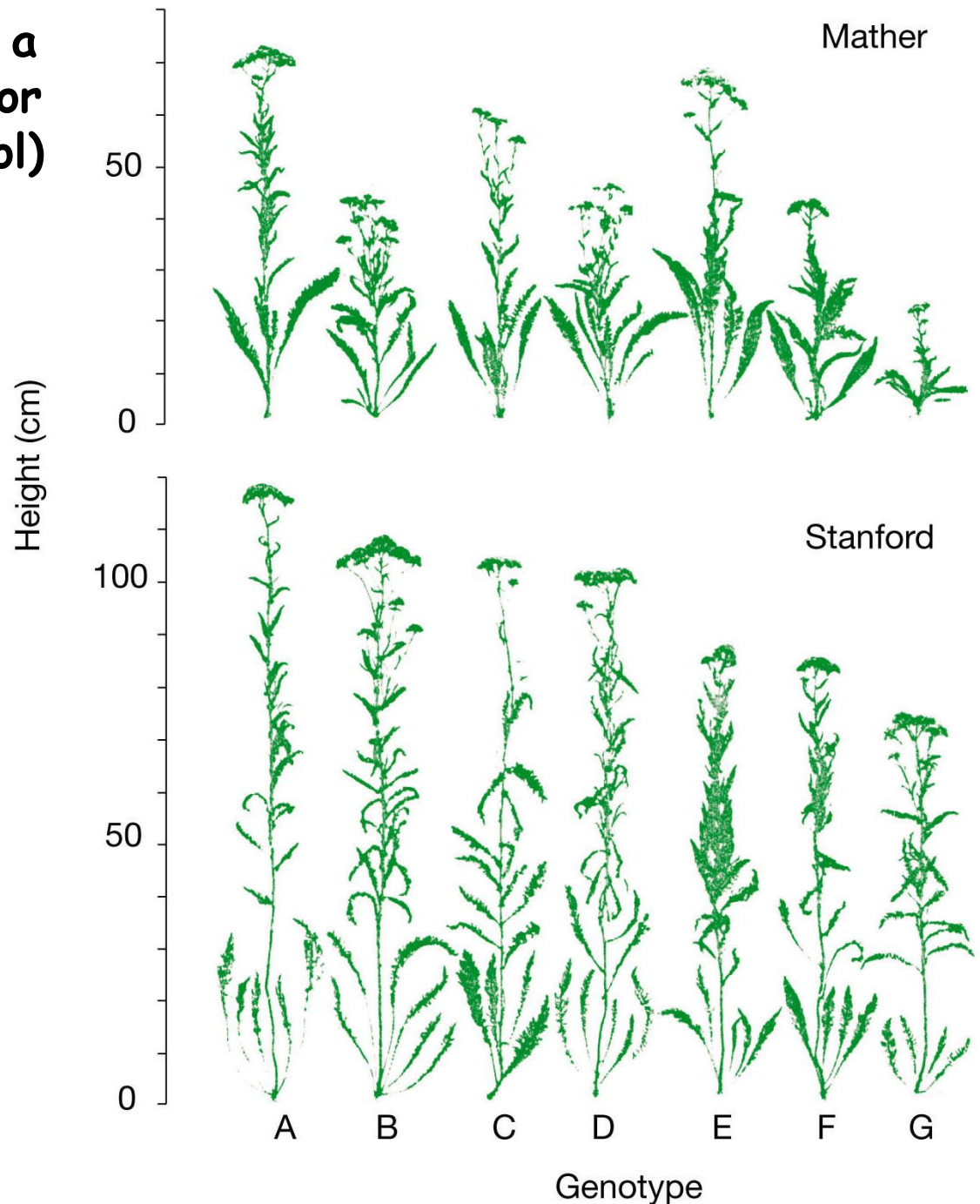
In C, K & H's experiment with *Achillea*, height was **highly heritable** within each environment.

But height in each environment was a **poor predictor** of height in the others, in two ways:

- (1) **Relative** heights differed between the environments, and
- (2) **All** genotypes grew **taller** at Stanford.

So differences **within** populations were largely determined by **genes**, but with **different outcomes** in each environment.

And the large average difference between populations was entirely non-genetic!

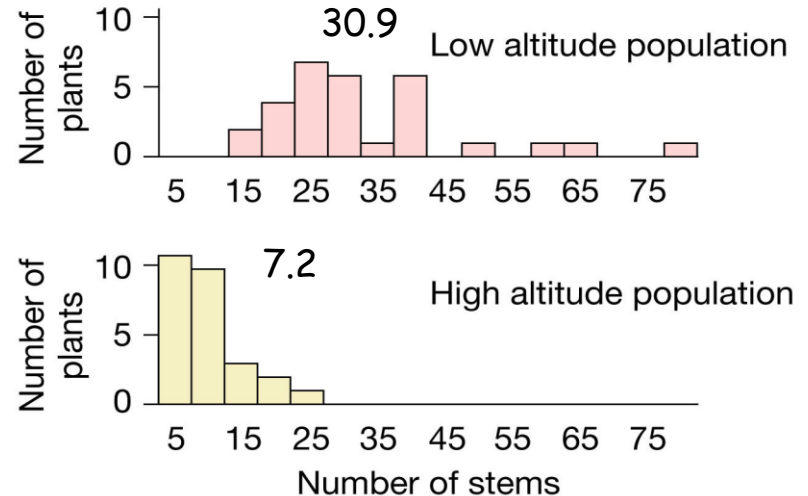


But populations *long separated* in different environments will adapt.

Achillea genotypes from low and high elevations responded *oppositely* to change!

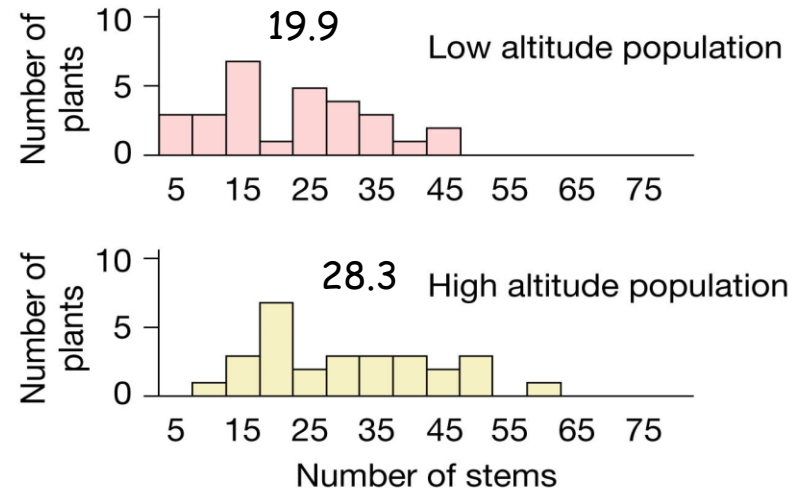
Grown at low altitude

When Clausen, Keck, and Hiesey (1948) grew *Achillea* from both populations in a garden at low altitude, the plants from the low altitude population made more stems (30.90 ± 2.73 versus 7.21 ± 1.08).



Grown at high altitude

When the researchers grew cuttings from the same plants in a garden at high altitude, the high altitude plants made more stems (28.32 ± 2.54 versus 19.89 ± 2.26).



Summary

- (1) There's *much quantitative-trait variation* in natural populations!
- (2) And much of it is *heritable* (i.e., selectable, because $V_A > 0$).
- (3) Populations evolve *rapidly* in ecological (short) time.
- (4) But *slowly* in evolutionary (long) time.
- (5) How can (2), (3) and (4) all be true at once?
- (6) Easily, if environments change frequently and genes flow not too rapidly between populations with different local optima.
- (7) GxE interaction (non-parallel norms of reaction) is probably common, and it will also tend to slow the loss of genetic variation.