Optimum selection and OU processes

29 November 2016.

Joe Felsenstein

Biology 550D

With selection ... life is harder

There is the “Breeder’s Equation” of Wright and Fisher (1920’s)

$$\Delta z = h^2 S$$

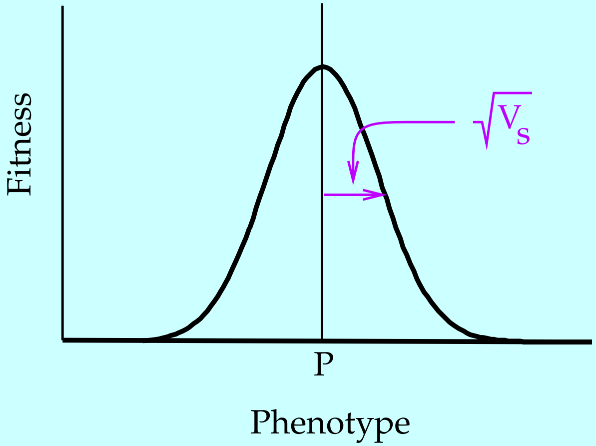
and Russ Lande’s (1976) recasting of that in terms of slopes of mean fitness surfaces:

$$S = V_P \frac{d \log(\bar{w})}{d\bar{x}}$$

$$\Delta z = (V_A/V_P)\, V_P \frac{d \log(\bar{w})}{d\bar{x}} = V_A \frac{d \log(\bar{w})}{d\bar{x}}$$

Note – it’s heritability times the slope of log of *mean* fitness with respect to *mean* phenotype. There is an exact multivariate analog of this equation.

Selection towards an optimum



If fitness as a function of phenotype is:

$$w(x) = \exp\left[-\frac{(x-p)^2}{2V_s}\right]$$

Then after some completing of squares and integrating, the change of mean phenotype “chases” the optimum:

$$m' - m = \frac{V_A}{V_s + V_P}\,(p-m)$$

(There is an exact matrix analog of this for multiple characters).

The Ornstein-Uhlenbeck process

(or rather, a random walk that comes interpolates it)

$$x_{t+1} \;=\; x_t \;+\; c\,(p - x_t) \;+\; \varepsilon_t$$

This is the same process as selection toward a peak value p plus genetic drift. A process that wanders around an optimum but is continually pulled toward it.

It is easy to show (take expectations termwise) that the expectation of x in the long run is p.

How variance accumulates in the OU process

Subtracting p from both sides

$$x_{t+1} - p = (1-c)(x_t - p) + \varepsilon_t$$

Squaring both sides and taking expectations

$$E[(x_{t+1} - p)^2] = (1-c)^2 E[(x_t - p)^2] + E[\varepsilon_t^2]$$

So that

$$\mathrm{Var}(x_{t+1}) = (1-c)^2 \mathrm{Var}(x_t) + \mathrm{Var}(\varepsilon)$$

How variance accumulates in the OU process

It is not too hard to show from this that

$$\mathrm{Var}(x_t) \;=\; \mathrm{Var}(\varepsilon)\,\left(1 + (1-c)^2 + (1-c)^4 + \ldots (1-c)^{2t}\right)$$

Or in the limit

$$\mathrm{Var}(x_\infty) \;=\; \frac{\mathrm{Var}(\varepsilon)}{1 \;-\; (1-c)^2}$$

If c is small, this is close to

$$\mathrm{Var}(x_\infty) \;=\; \frac{\mathrm{Var}(\varepsilon)}{2c}$$

(Now we run the simulation of the OU process)

Sources of evolutionary correlation among characters

Variation (and covariation) in change of characters occurs for two reasons:

- **Genetic covariances.** (the same loci affect two or more traits)

Sources of evolutionary correlation among characters

Variation (and covariation) in change of characters occurs for two reasons:

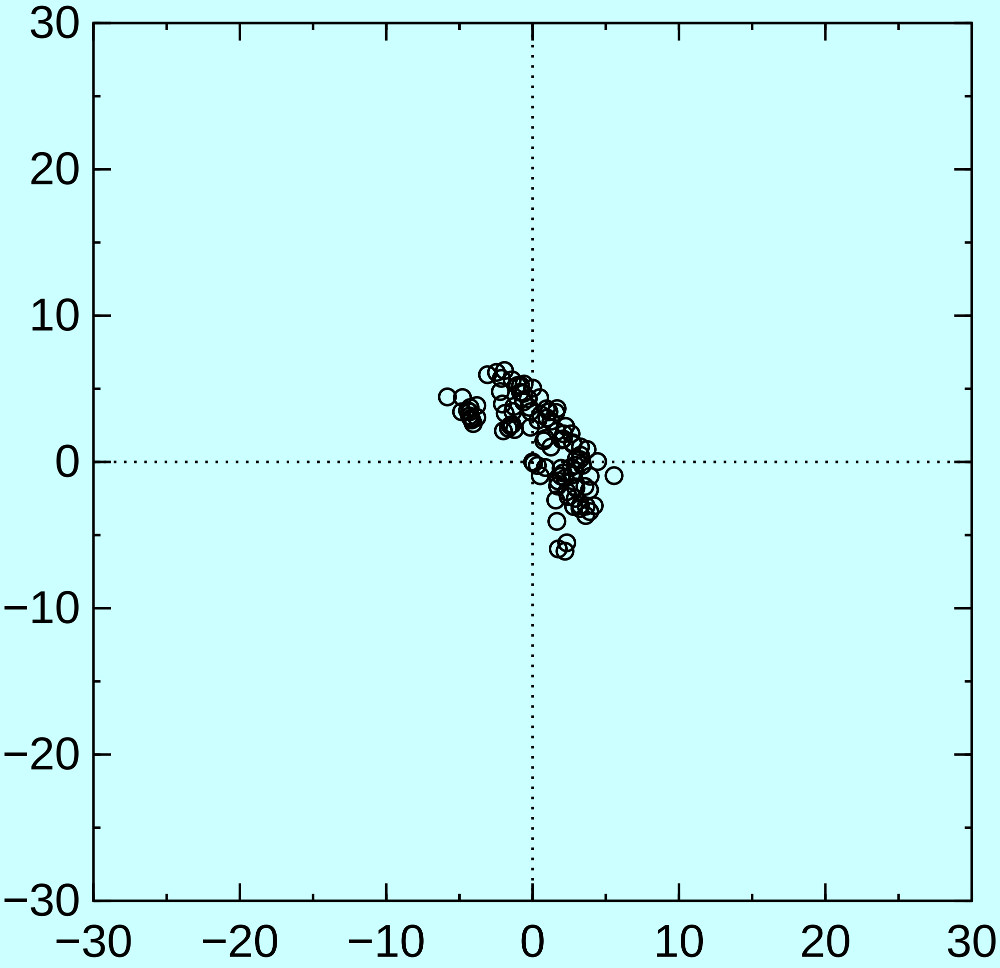
- **Genetic covariances.** (the same loci affect two or more traits)
- **Selective covariances** (Tedin, 1926; Stebbins 1950). The same environmental conditions select changes in two or more traits – even though they may have no genetic covariance.

A case that has received too little attention

- Suppose characters `x` and `y` are genetically correlated.
- and `y` is under optimum selection, but `x` is the one we observe.
- What will we see? In effect, the sum (actually, a weighted average) of an Ornstein-Uhlenbeck process and Brownian Motion.
- So Brownian motion restricted in the short run but not in the long run.

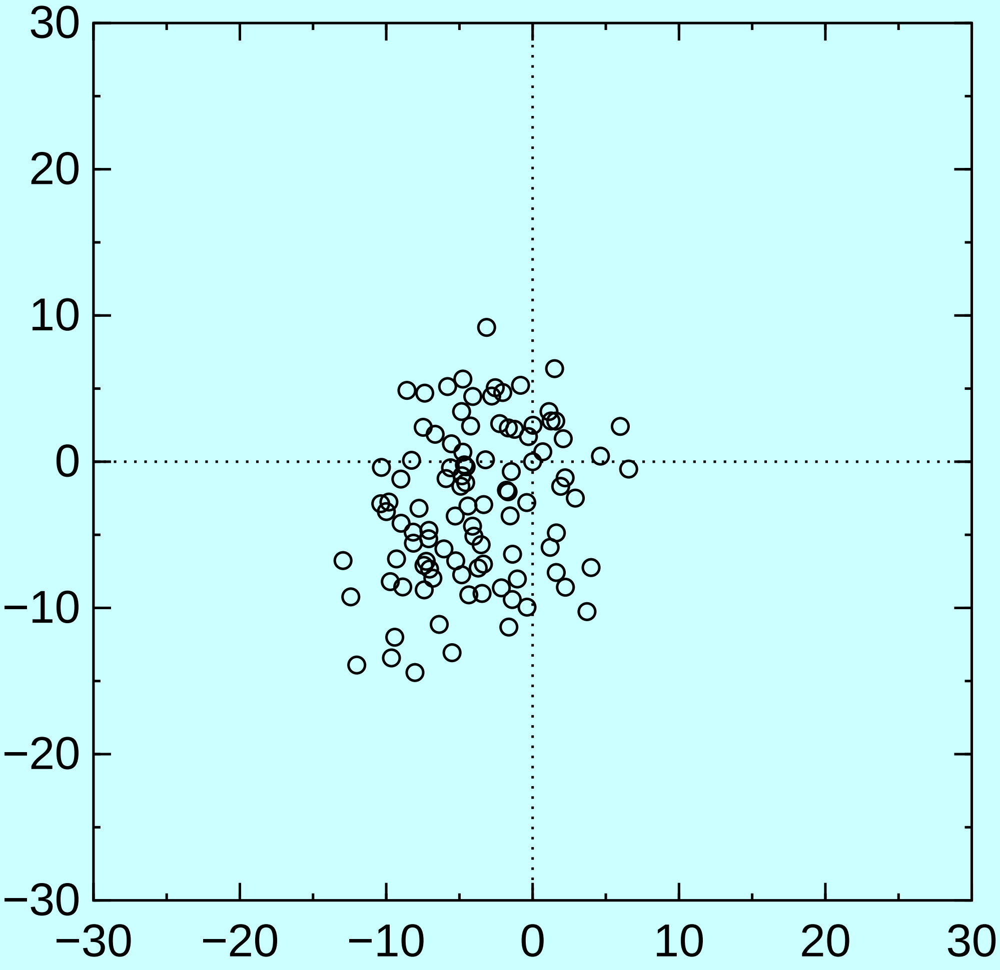
Most models so far do not allow for characters that are observed to covary with those that aren't observed.

Chasing a peak, simulated with two characters



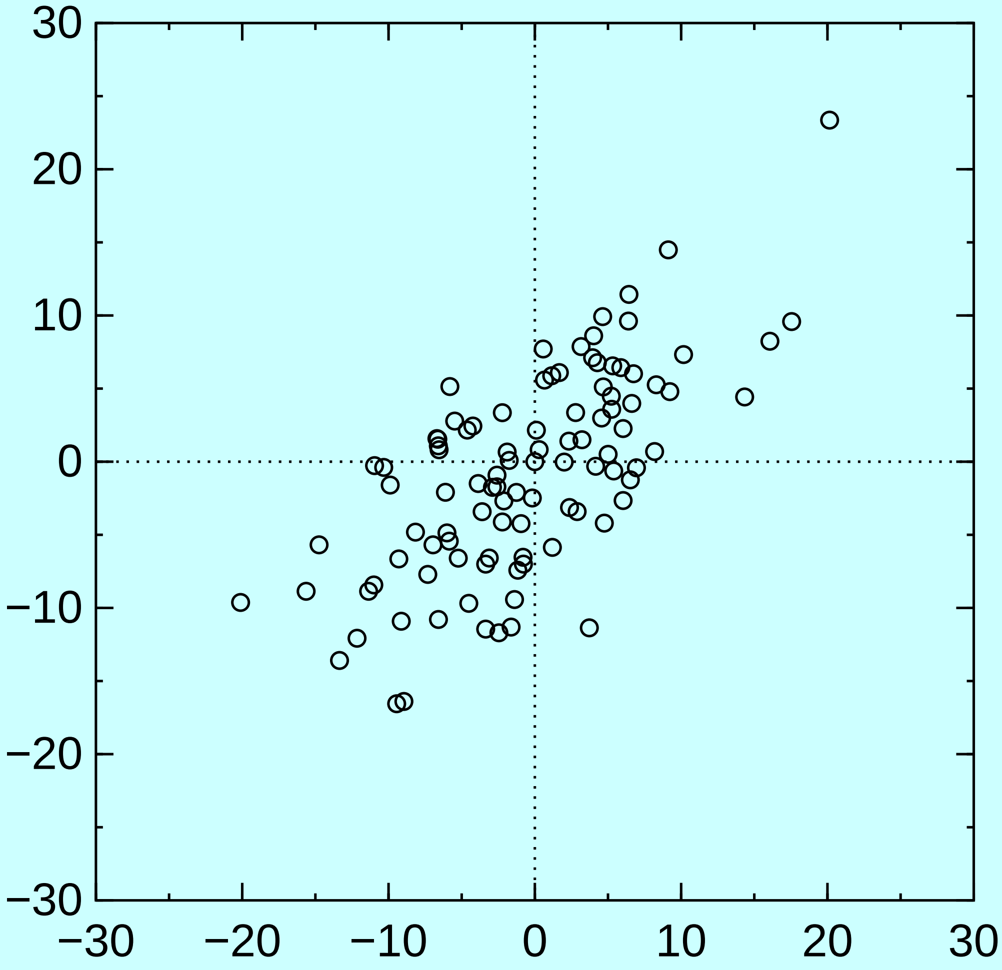
Genetic covariances assumed negative, but the wanderings of the adaptive peaks assumed positively correlated. After a while (every generation up to generation 100), the wanderings of the peaks start to be influential.

Chasing a peak, simulated with two characters



Genetic covariances assumed negative, but the wanderings of the adaptive peaks assumed positively correlated. After a while (every 10th generation up to generation 1000), the wanderings of the peaks start to be influential.

Chasing a peak, simulated with two characters



Genetic covariances assumed negative, but the wanderings of the adaptive peaks assumed positively correlated. In the long run (every 100th generation up to generation 10,000) the means go mostly where the peaks go.

Other issues to think about

- What about multivariate drift and selection?
- What if the peak moves?
- What if the peak continues to move (and what is a natural assumption for that process)?
- What happens at a speciation – do both daughter species follow the same adaptive peak, or different ones?

A little algebra showing the effect of selective covariance

If we start from the familiar “Breeder’s Equation” of quantitative genetics:

$$\Delta \mathsf{z} = \mathsf{h}^2 \, \mathsf{S}$$

it has long been known to have a multivariate version:

$$\boldsymbol{\Delta z} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S}$$

Multiplying $\boldsymbol{\Delta z}$ by its transpose:

$$\boldsymbol{\Delta z}\boldsymbol{\Delta z}^{\mathsf{T}} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S}\mathbf{S}^{\mathsf{T}}\mathbf{P}^{-1}\mathbf{G}$$

and taking expectations (treating $\mathbf{G}$ and $\mathbf{P}$ as constants) we get for the mean squares:

$$\mathsf{E}[\boldsymbol{\Delta z}\boldsymbol{\Delta z}^{\mathsf{T}}] = \mathbf{G}\mathbf{P}^{-1}\mathsf{E}[\mathbf{S}\mathbf{S}^{\mathsf{T}}]\mathbf{P}^{-1}\mathbf{G}$$

(Felsenstein, 1988)

References for multivariate Brownian motion

Felsenstein, J. 2004. *Inferring Phylogenies.* Sinauer Associates, Sunderland, Massachusetts. **[See particularly chapters 23, 24, 25]**

Felsenstein, J. 1988. Phylogenies and quantitative characters. *Annual Review of Ecology and Systematics* **19:** 445-471. **[Review with mention of usefulness of threshold model]**

Felsenstein, J. 2002. Quantitative characters, phylogenies, and morphometrics.pp. 27-44 in *Morphology, Shape, and Phylogenetics*, ed. N. MacLeod. Systematics Association Special Volume Series 64. Taylor and Francis, London. **[Review repeating 1988 material and going into some more detail on the question of threshold models.]**

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30:** 314-334. **[Lande's classic paper on drift versus optimum selection]**

Lande, R. 1979. The quantitative genetic analysis of multivariate evolution, applied to brain-body size allometry. *Evolution* **33:** 402-416.

References

Lande, R. 1980. The genetic covariance between characters maintained by pleiotropic mutations. *Genetics* **94:** 203-215.

Lynch, M. and W. G. Hill. 1986. Phenotypic evolution by neutral mutation. *Evolution* **40:** 915-935.

Stebbins, G. L. 1950. *Variation and Evolution in Plants*. Columbia University Press, New York. **[Describes selective covariance and cites Tedin (1925) for it]**

Tedin, 0. 1925. Vererbung, Variation, und Systematik der Gattung *Camelina*. *Hereditas* **6:** 275-386.

Armbruster, W. S. 1996. Causes of covariation of phenotypic traits among populations. *Journal of Evolutionary Biology* **9:** 261-276. **[Good exposition of selective covariance]**