Variation in natural populations

1) How much phenotypic variation is present in natural populations?

2) What is the genetic basis of variation?

3) Genetic covariance

4) Genetic and non-genetic polymorphisms

5) Supergenes in natural populations

6) What maintains genetic variation in natural populations?
1) How much phenotypic variation is present?

Coefficient of variation $100(\sigma/\bar{x})$ is 2 to 4% for most birds but is greater in many other organisms.
Continuous phenotypic variance has two main components:

\[ V_P = V_G + V_E \]

2) What is the genetic basis of variation?
2) What is the genetic basis of variation?

Quantitative genetic model of continuous variation

\[ V_P = V_G + V_E \]

Total phenotypic variance among individuals in the population (measured directly)

“Environmental” variance, which means everything else: true environmental variance, but also developmental noise, non-additive genetic variance

Beak depth

Additive genetic variance among individuals.

Additive = the genetic variance component determining the resemblance of offspring to their parents.
2) What is the genetic basis of variation?

Heritability: the fraction of total phenotypic variance that is additive genetic

\[ h^2 = \frac{V_G}{V_P} \]
Recall: example of directional natural selection

\[ S = \bar{Z}_{after} - \bar{Z}_{before} = 1 \]

\[ \Delta \bar{Z}_{offspring} = h^2 S = 0.2 \]
Cross-fostering experiment on Mandarte Island song sparrows

Beak depths (mm) of offspring compared with the beak depth of their true parents and their foster parents.

“mid-parent” is the average of male and female parent measurements

Smith and Dhondt (1980) Evolution
2) What is the genetic basis of variation?

Most continuously-varying traits appear to be heritable.

**Figure 3** The cumulative frequency distributions of the four trait categories (L = life history, B = behaviour, P = physiology, and M = morphology) for the entire data set. Note that data points are joined by straight lines.

Mousseau and Roff (1987) Heredity
2) What is the genetic basis of variation?

Example of a non-genetic source of variation: maternal effects

<table>
<thead>
<tr>
<th>Apparent “heritability” of daughters’ pronotum width in O.taurus</th>
<th>h²</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heritability of offspring pronotum width estimated using resemblance to father</td>
<td>0.020</td>
<td>0.069</td>
</tr>
<tr>
<td>Heritability of offspring pronotum width estimated using resemblance to mother</td>
<td>0.279</td>
<td>0.186</td>
</tr>
</tbody>
</table>

"Dung beetles belonging to the genus Onthophagus provision offspring before hatching. During reproduction, females remove portions of dung and pack them into the blind end of tunnels excavated beneath the dung pad. A single egg is deposited into an egg chamber, which is then sealed; one egg and its associated dung provision constitutes a brood mass and represents the entire resource base that is available to a larvae during development."

Hunt and Simmons (2002) PNAS
3) Genetic covariance

Evolutionary significance of genetic covariance

Main cause of genetic covariance is thought to be pleiotropy

Phenotypic covariance

Genetic covariance

Conner and Via (1993) Evolution
4) Genetic and non-genetic polymorphisms

Polymorphism: discontinuous variation within a population

Examples of mainly non-genetic polymorphisms

A. 
B. 

The two morphs of *Chthamalus anisopoma*
(A) The conical morph; (B) the bent morph

If individual herbivorous tadpoles of the spadefoot toad *Scaphiopus multiplicatus*, eat a fairy shrimp, they transform into a large carnivore and even a cannibal

Pfennig (1992) Evolution
Lively (1986) Ecology
4) Genetic and non-genetic polymorphisms

Examples of mainly genetic polymorphisms

The black-bellied seedcracker exhibits a non-sex related polymorphism in bill size caused by a single locus having two alleles, “small” is dominant over “large” (gene not yet known).

The threespine stickleback in Kennedy Lake exhibits a polymorphism in bony lateral plates mainly determined by the major gene *Ectodysplasin (Eda).*

Smith (1993) Nature

Marchinko et al (2014) Current Biology
Do we need to know the genes underlying polymorphisms?
Genes might help to identify mechanisms of selection on traits

This study tracked the frequency of the low-armor *Eda* allele in four replicate pond populations of stickleback (different colored lines) that all started at frequency 0.5. *Eda* is the major gene underlying armor variation.

Samples were taken at different time points as each cohort of fish developed and grew into adults (and then reproduced).

The study found that there were strong shifts in allele frequency at *Eda* even before the fish had fully developed their armor. These shifts result from differential mortality. This suggested that armor variation was not the main cause of shifts at *Eda*. We now know that *Eda* also affects sensory perception and schooling behavior.

Possibly, armor changed over the course of the experiment only because it is correlated with the real trait under natural selection.

Barrett et al. (2008) Science
4) Supergenes in natural populations

Some complex phenotypic polymorphisms are determined by variation at a supergene: a group of linked genes inherited together

A supergene underlies a polymorphism in male ruffs with three morphs: dark “independents” white “satellites” and female mimicking “faeders” (left to right).

Pennisi et al (2017) Science (Photo by C. Küpper & D. Lank)
4) Supergenes in natural populations

Reconstruction of supergene evolution in ruff

Examples usually involve a similar mechanism to prevent the breakup of linked genes by recombination (crossing over).

Linked genes are held together on a chromosomal inversion, which largely prevents crossing-over between opposites in the inverted region, allowing groups of alleles that function together to remain associated.

In this way a complex of traits can be inherited together as a simple genetic polymorphism.

4) Supergenes in natural populations

Social polymorphism determined by independently-evolved inversions in fire ant and alpine silver ant

<table>
<thead>
<tr>
<th>Single queen colony</th>
<th>Multiple queen colony</th>
</tr>
</thead>
<tbody>
<tr>
<td>One</td>
<td>More than one</td>
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<tr>
<td>Larger</td>
<td>Queen size</td>
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<tr>
<td>Larger</td>
<td>Smaller</td>
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<td>Independent</td>
<td>Colony founding</td>
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<tr>
<td>Independent / Dependent</td>
<td></td>
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Color and pattern polymorphism in *Heliconius numata*

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Color/behavior polymorphism in white throated sparrow

*White-throated sparrow* (*Zonotrichia albicollis*)

- Tan morph
- White morph

5) What maintains genetic variation in natural populations?

Hypotheses

I) Mutation-selection balance

ii) Balancing selection (net advantage of heterozygotes)

iii) Divergent natural selection with gene flow

iv) Frequency-dependent selection