NB: NOTES USED TO JUDGE QUESTION ANSWERS for B242 Exam 2004

Q. 2. Is the study of hybrid zones the key to understanding speciation? Discuss why or why not.

Hybrid zones: narrow zones of contact between divergent forms or even species.
Many clines (1-gene 1 cline) clustered together in space.

Many species and/or races are distributed in **parapatry**, narrow hybrid zones between them.
Examples: chromosomal races of mammals, warningly coloured butterflies, sexually selected birds

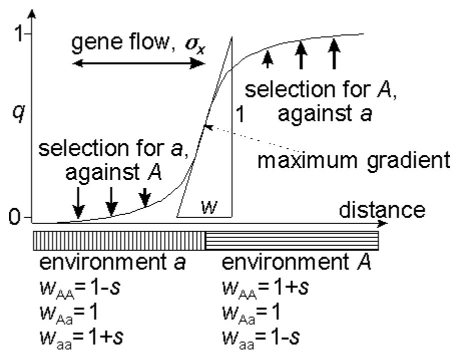
Genetic divergence and speciation
Speciation involves genetic divergence; usually over a long time period.
Cannot usually study speciation directly; we only have access to present-day populations. But we *can* study spatial variation in gene frequencies.
Dispersal is spatially limited, so distant populations share ancestry less recently than adjacent populations
Spatial variation therefore related to temporal variation in gene frequencies.
Spatial variation, understanding of the time course of genetic divergence and speciation.
Many newly formed pairs of species have parapatric or allopatric distributions.

Spatial differences in gene frequencies may represent speciation in progress
Parapatric distributions and *hybrid zones* or *contact zones* within species: a first step in speciation.
Many intermediates between slight genetic differentiation and separate species occur in parapatry.

Genetic variation across a geographic area
Any *consistent* change in gene frequency heritable phenotype, across a geographical range -- known as a *cline*.
Clines occur because dispersal across a region is limited, because the whole geographical area does not form a single *panmictic population*.
(Population geneticists often call dispersal *migration*, but do not mean the kind where birds return after migration to near their parents nest!)
Dispersal also called *gene flow*, though we usually mean *genotype flow*).

Causes of clines

a) *Clines produced by selection/migration balance - EXTRINSIC selection*
Extrinsic or *environmental selection* is imposed by the environment directly.
selection will set up a cline in gene or phenotype frequency.



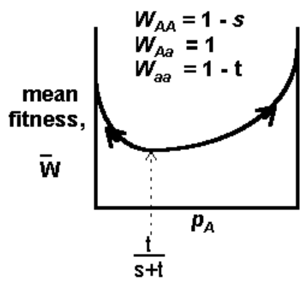
At equilibrium, the width of a cline is proportional to dispersal divided by the sq. root of selection:

$$w = 1.7\frac{\sigma}{\sqrt{s}}$$

1) Width of cline should scale directly to dispersal distance; cline wider as dispersal increases
2) Stronger selection leads to narrower cline
i.e. $w \propto f$(selection)

b) Clines and hybrid zones produced by selection- migration balance -- INTRINSIC selection

i) Heterozygous disadvantage
Heterozygous disadvantage creates a kind of *disruptive selection*.
Two peaks in mean fitness, known as *adaptive peaks*;
fixation for *A*, and fixation for *a*.



$$w = 2.8\frac{\sigma}{\sqrt{s'}}$$, ... where s' is average of s & t.

ii) Frequency-dependent selection
For example, warning colour:
iii) Epistatic and disruptive selection
Disruptive selection; a kind of *intrinsic selection* caused by the *environment*.
Selection can favour a bimodal phenotypic distribution, or two *adaptive peaks* simultaneously.

Disruptive selection for different adaptive peaks also produces epistasis
Bimodal or disruptive selection implies *epistasis*, must be due to non-additive interactions in selection between genes.

Sexual selection
Also may cause epistatic/disruptive selection:
genes for mate choice strongly epistatic with genes for the traits being chosen.

Typically, hybrid zones are stabilized by a combination of intrinsic/extrinsic effects. Different effects might act on different gene clines.

How understanding clines and hybrid zones leads to some general rules of speciation
1) Speciation is *gradual* (usually), and involves *many loci*. Evidence:
Hybrid zones: hybridising forms differ at many loci, even though not separate species.
Species can overlap without losing identity in parapatry or sympatry; hybridizing races do not.
⇒ species should differ at even more loci. (See Ayala's work in the 1970s on *Drosophila*).
(A major exception to "gradual speciation" rule is speciation via polyploidy).

2) Speciation involves *epistasis*.
To maintain bimodal distribution of genotypes, intermediates must be unfit.
For example, *AABB* and *aabb* have high fitness, whereas *AaBb* and *AAbb* genotypes are less fit.
A and *B* collaborate, or are *epistatic*.

3) *No clear geographic* rule for divergence
Species differ at genes under *intrinsic* or *extrinsic* selection against hybrids.
Extrinsic selection caused by variable *environment*. *Intrinsic* selection caused by *heterozygous disadvantage*, *frequency dependent selection* against rare forms, and, very importantly, *epistatic selection*.

Geography of speciation
Intrinsic selection, extrinsic selection, mate choice.
…just what we have been learning about.

Cline theory: $w = 1.73\sigma/\sqrt{s}$.

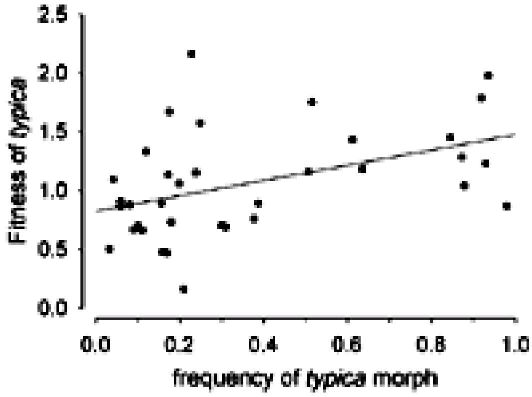
So, divergence & speciation possible in *parapatry*.
No requirement for complete geographic isolation.

4) *Species, geographic races, local morphs are part of a continuum*.
No fundamental difference between species and races and morphs genetically. A continuum.
Species just a little bit more divergence
And bimodal when in contact.

5) *Reinforcement*.
Finally, studies have shown that reinforcement may occur in areas of overlap and hybrid zones, where overlapping populations avoid mating with one another, whereas allopatric, non-overlapping populations can be made to mate with each other in the lab.

Q. 5 "We must discard *Biston* as a well-understood example of natural selection in action, although it is clearly a case of evolution". What is the author talking about? Defend your view of the matter.

Peppered moth melanism – the classic story of natural selection in the wild
JBS Haldane calculated long ago that the melanics must have had about 50% higher survival than typical mottled forms to explain the rapid rise in melanic gene frequency.



More recently, over 30 experiments by many different scientists across Britain were performed to investigate selection. Overall, they showed strong selection against melanics in sooty areas, and strong selection against melanics in areas unaffected by pollution. Other experiments with birds showed birds could detect moths in accordance with their visual background matching.

The peppered moth story – refuted?

Today, suddenly, doubt that peppered moth melanism is due to bird predation is surfacing.
Critical articles about bird predation story.
Biography of Kettlewell suggesting he faked his story.
Arguments that the peppered moth does not rest on tree trunks. (Actually, they tend to rest higher up, under the major branches, but this is still on bark, and the same arguments probably apply). That the UV colouring of the moth is different to that of the lichen on which it rests. (But the bird experiments show that the camouflage is actually effective).

In my view ...
The hooha is based on no new experiments or discoveries; it is retrospective criticism of the original work, almost entirely by people who know nothing about the work. There are are no particularly good pieces of evidence that the old experiments are wrong. Noone has tried to repeat the experiments (indeed this would be rather difficult,now since there are hardly any melanics left, and sooty tree trunks are largely a thing of the past). It is as though people just seemed bored with the same old story, and want it to be wrong.

Needless to say, the students haven't had time to read all the literature about this subject, so I gave them good marks if they remembered some of the criticisms and counterarguments, regardless of their overall take on the controversy.

Q. 8. List and describe three advances in *evolutionary* biology that could not have been made without molecular biology techniques invented since the 1950s.

Straightforward question: so many answers that I can't possibly list them all. However, they must be molecular (for instance, one student thought that linkage disequilibria was one such advance that led to finding of genetic disease genes, but I can't really count that without any mention of the molecular techniques to be used in linkage disequilibrium analysis), and they must be evolutionary (so finding disease genes doesn't count).

Examples include: neutral theory due to discoveries of protein polymorphisms, discovery of genome evolution and introns, use of molecular genetic data in phylogeny reconstruction, in understanding gene flow among natural populations, in understanding genetic drift in small populations in conservation genetics (an evolutionary problem, in my view), discovery and understanding of the evolution of just about any gene, such as insecticide resistance genes, discovery of positive selection on amino acids by comparison with third-base pair position evolutionary rates, and so on.