What is adaptation?

- There are several definitions of adaptation
- Gould and Vrba (1982)
  - Adaptation: a trait built by natural selection for its current biological role
    - Two criteria:
      - The trait enhances organismal performance (criterion of current utility)
      - The trait evolved via natural selection for its current use (criterion of historical genesis)
    - Exaptation: trait whose evolutionary origin was not related to its current biological role

Baum and Larson 1991
What is adaptation?

• Sober (1984)
  – Questioned the relevance of current utility
  – Emphasized the criterion of historical genesis
  – Even if it falls out of current utility, it may have been adaptive in the past

“Adaptation and fitness are complementary concepts. The former looks to the past, reflecting the kind of history a trait had. The latter looks to the future, indicating the changes that organisms have for survival and reproductive success. These retrospective and prospective concepts are mutually independent. An adaptation may cause problems for the organisms that may mean that an adaptation is no longer advantageous.”

Baum and Larson 1991

What is adaptation?

• Fisher (1985)
  – Historical genesis is irrelevant
  – Emphasizes criterion of current utility
  – If adaptations are by definition built by natural selection, natural selection cannot be used to explain the phenomenon of adaptation

• Coddington (1988)
  – Apomorphic structure or function promoted by natural selection
  – Performance of derived state are compared to the appropriate primitive condition
  – Exaptations are simply adaptations at another level

Baum and Larson 1991
• Regardless of the definition:
  – Current utility is useful for developing causal hypotheses of trait origin
  – Historical genesis is useful for studying the process of adaptation

Convergent and Parallel Evolution

• Similarity in morphology may be due to:
  – Common ancestry
    • Ancestral condition was passed on to daughter lineages
  – Convergent or parallel evolution
    • Similar selective pressures towards taxa that occupy the same niche
  – Random chance
• A major challenge in evolutionary biology and phylogenetics is distinguishing these causes of similarity
Convergent and Parallel Evolution

• Convergent evolution
  – This similarity is caused by adaptive evolution
  – Similarity between organisms is not due to common ancestry
  – Lineages with different ancestral morphologies can evolve in different directions towards the same adaptive phenotype
  – Changes from a different ancestral amino acid to the same descendent amino acid along an independent lineage

Convergent and Parallel Evolution

– Convergence is a critical issue in systematics because it can mislead phylogeny reconstruction
  • Analyses may group distantly related organisms due to similarity from selective pressure rather than similarity from common ancestry
  – Distantly related species with independently derived similarity in similar environments are not necessarily convergent
    • Exaptation
    • Species evolve similarity for a different reason
    • These pre-existing similarities permit use for the same function or occupation of the same habitat
Example of convergent evolution

Convergent evolution of body plans in marsupial and placental mammals

- Mole and marsupial mole: fusiform body and modified forelimbs
- Anteater and numbat: claws and long sticky tongues for myrmecophagy
- Mouse and marsupial mouse: small foraging mammals
- Lemur and spotted cuscus: elongated fingers to get insects from trees
- Flying squirrel and flying phalanger: gliders with skin stretched between limbs to increase surface area
- Bobcat and Tasmanian tiger cat: small carnivore, large canines
- Wolf and Tasmanian wolf: large carnivore, large canines, long limbs

Convergent and Parallel Evolution

- Parallel evolution
  - Lineages with the same ancestral morphology may independently evolve in the same direction towards the same endpoint
  - Produces similarity through independent modifications of the same feature
  - Amino acid changes along independent lineages may have occurred from the same ancestral amino acid
Example of parallel evolution

Parallel evolution of crab-like forms in arthropods

Red branches indicate multiple origins of crab-like structures

Multiple origins are likely the result of similar changes in shared developmental pathways

- How do we know whether similarities are due to adaptive evolution (convergence, parallelism), shared ancestry, or chance?
- **Use phylogenetic methods to test evolutionary hypotheses**
  - Kornegay et al. 1994, Zhang and Kumar 1997: stomach lysozyme
  - Baum and Larson 1991: arboreal salamanders
  - Wiens et al. 2003: cave-dwelling salamanders
  - Revell et al. 2007: rock-dwelling lizards
Stomach Lysozyme Evolution

- Lysozyme:
  - Bacteriolytic enzymes expressed in macrophages in tears, saliva, avian egg white, mammal milk
  - Cleaves $\beta(1-4)$ glycosidic bond between $N$-acetyl glucoseamine and $N$-acetyl muramic acid in cell walls of eubacteria, resulting in cell lysis
  - First line of defense against bacterial invaders
  - Two groups:
    - Conventional lysozyme and calcium-building lysozyme
    - Arose from gene duplication prior to divergence of birds and mammals
- Stomach lysozyme
  - Lysozyme excreted in foregut fermenters to free nutrients from bacteria
  - Arose three times independently: ruminants, langur monkeys, hoatzin
- Question: Did stomach lysozyme arise independently as a result of selection or by random chance?

Kornegay et al. 1994; Zhang and Kumar 1997
• Kornegay et al. (1994)
  – Obtained amino acid sequences of stomach lysozymes
  – Constructed a phylogeny from amino acid sequence data

Parallel and convergent amino acid replacements are shown here
D75 and N87 occurred in all three lineages

– Obtained amino acid sequences of stomach lysozymes
– Constructed a phylogeny from amino acid sequence data
– Hoatzin lysozyme has more substitutions than sister pigeon
  • Accelerated evolution due to selection
– Five amino acid positions have experienced parallel/convergent replacements
  • Adaptations enabling lysozyme to function in hostile stomach environment
  • Three of these are on the surface of the enzyme and are exposed to the acidic environment of the stomach
  • Meets **current utility** criterion
    – Better performance of lysozyme at low pH
    – Resistance to proteolytic pepsin

Kornegay et al. 1994
• Zhang and Kumar (1997)
  – More rigorous study of lysozyme evolution
  – Two steps to study adaptive evolution:
    1. **Identify the amino acid sites that have experienced identical substitutions**
       – Reconstruct ancestral amino acids at interior nodes
    2. **Test whether these changes arose due to natural selection or random chance**
       – Protein evolution is stochastic with 20 states at each site
       – Use a **statistical model** of protein evolution
  – Study taxa:
    • Stomach lysozyme of langur, cow, hoatzin
    • Nonstomach lysozyme of human, baboon, rat, chicken, pigeon, horse
- Statistical test: probability of observing a given number of convergent change sites by chance

\[
\phi = \sum_{i=0}^{m} \frac{m!}{i!(m-i)!} f_c^i (1 - f_c)^{m-i}
\]

\(\phi\): probability of observing \(n_c\) or more convergent changes by chance

\(i\): amino acid

\(m\): length of amino acid sequence

\(n_c\): observed number of convergent change sites

\(f_c\): probability that a site is a convergent change site
  - Incorporates branch length
  - Incorporates model of substitution

- This method can also be applied to parallel sites

Zhang and Kumar 1997

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Stomach lysozymes are shown in bold

Zhang and Kumar 1997

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Sites 75 and 87: parallel-change sites
- Site 75: D in all stomach lysozymes, N in all nonstomach lysozymes
- Site 87: N in all stomach lysozymes, no N in nonstomach lysozymes

- No convergent change sites were identified
- Other sites identified by Kornegay et al. (1994) are random homoplasy
- Not all of the five sites identified by Kornegay et al. (1994) meet the historical genesis criterion
Baum and Larson (1991)

- Propose a method of testing evolutionary hypotheses that combines historical genesis and current utility aspects
- Current utility
  - Assess phylogenetic congruence between change in form and change in fitness-related variables
- Historical genesis
  - Incorporates the concept of “selective regime”
  - Difficult in practice to determine all components
  - Consider only critical aspects of environment/organism interaction

1. **Phylogeny reconstruction**
   - Do not use characters being studied to construct phylogeny
   - If testing whether a morphological feature is adaptive, use genetic data
2. **Score the character states**
   - Be sure that character states are homologous
3. **Score the selective regime**
   - Abiotic factors: climate, geography
   - Biotic environmental factors: interactions with other species, predator-prey relationship, diet
   - Organismal: flight capability, climbing ability
   - Combination based on natural history studies
4. **Partition character changes on a phylogeny**
   - Locate character state changes on phylogeny by using parsimony

Baum and Larson 1991
5. **Infer selective regimes of ancestral lineages**
   - Paleontology, biogeographic, climatic data
   - If no extrinsic data, use parsimony to reconstruct ancestral regime

6. **Assess current utility**
   - Induce ancestral character state in study organism
   - Compare focal taxon to a sister that lacks feature being studied but shares selective regime
   - Use mathematical models based upon knowledge of organismal biology to predict consequences of character state change

7. **Classify traits into categories of utility/historical genesis**
   - Did the trait evolve on an internal branch having the same selective regime as the focal taxon? Use the phylogeny
   - What is the current biological role?

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**Case study: evolution of traits associated with arboreality in the salamander genus *Aneides***

- Phylogeny reconstruction
  - Tree based on immunological and electrophoretic protein comparisons

- Score the characters
  - Tarsal organization: small (H) or large (h)
  - Carpal organization: broad (I) or narrow (i)
  - Terminal phalanges: rounded (J) or flattened (j)
  - Otic crests: poorly (M) or well (m) developed

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Baum and Larson 1991
Case study: evolution of traits associated with arboreality in the salamander genus *Aneides*

1. **Phylogeny reconstruction**
   - Tree based on immunological and electrophoretic protein comparisons

2. **Score the character states**
   - Tarsal organization: small (H) or large (h) fifth tarsal
   - Carpal organization: broad (I) or narrow (i)
   - Terminal phalanges: rounded (J) or flattened (j)
   - Otic crests: poorly (M) or well (m) developed

<table>
<thead>
<tr>
<th>Character</th>
<th><em>P. boreas</em></th>
<th><em>A. aeneus</em></th>
<th><em>A. baeri</em></th>
<th><em>A. ferreus</em></th>
<th><em>A. flavipunctatus</em></th>
<th><em>A. lugubris</em></th>
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</thead>
<tbody>
<tr>
<td>H. Tarsal organization</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>I. Carpal organization</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>J. Terminal phalanges</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>M. Otic crests</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Baum and Larson 1991

3. **Score the selective regime**
   - Selective regime: terrestrial or scansorial (arboreal)

4. **Partition character changes on a phylogeny**
   - Locate character state changes on phylogeny by using parsimony

5. **Infer selective regimes of ancestral lineages**
   - Transition from terrestrial to scansorial along lineage of *Aneides* and reversal in *A. flavipunctatus*

Baum and Larson 1991
6. **Assess current utility**
   - Impractical to experimentally manipulate trait or compare sister taxa
   - Mechanical and mathematical models of traits

7. **Classify traits into categories of utility/historical genesis**
   - Traits h, i, j arose on same branch as the switch in selective regime
   - Trait m arose on same branch as aggression and scansorial feeding, both which are potential roles for this adaptation

Wiens et al. (2003)

- Three pieces of evidence are needed to identify a convergent adaptation
  1. **Strong morphological support for a clade that unites the taxa from the similar selective environment**
     - Statistical support rules out the possibility of association between species due to random homoplasy or poor character sampling
  2. **Evidence that the convergent characters are associated with the selective environment**
     - This rules out the possibility of association due to shared homoplasies, weak taxon sampling, fixation due to drift
  3. **Phylogenetic evidence that the species sharing the selective environment are not a monophyletic group**
     - This rules out the possibility that the similarity is plesiomorphic
• Case study: cave-dwelling salamanders

– Genus *Eurycea*

– Edwards plateau (TX)

– 13 Plethodontid salamanders, monophyletic radiation

– Surface-dwelling species are extremely similar morphologically

– Cave-dwelling species show varying degrees of morphological modification that are associated with subterranean life

  • Broader and flatter head, reduced pigmentation and eye size

– Combined analysis of morphology, allozymes, mitochondrial cytochrome-*b*

– Question: Do cave-dwelling species in this genus meet the three criteria for convergence?

*Wiens et al. 2003*
Species whose morphologies are associated with caves are shown in **bold**

Morphology places *E. tridentifera* and *E. rathbuni* in a clade —79% bootstrap value

Genetic evidence supports that *E. tridentifera* and *E. rathbuni* are distantly related within the genus

Wiens et al. 2003

1. Strong morphological support for a clade that unites the taxa that share the similar selective environment
   - The clade uniting *E. rathbuni* and *E. tridentifera* is well supported, with a bootstrap value of 79%.
   - The rathbuni-tridentifera clade is not a result of the stochastic effects of random homoplasy and undersampling of characters

2. Evidence that the convergent characters are associated with the selective environment
   - Significant association of convergent traits with the exclusive use of caves
   - Strongest support for rathbuni-tridentifera clade: reduced eye size, loss of orbitosphenoid bone, reduced number of vertebrae

3. Phylogenetic evidence that the species sharing the selective environment are not a monophyletic group
   - The genetic data strongly support a distant relationship between *E. tridentifera* and *E. rathbuni*
   - Placement of *E. tridentifera* in a clade with six other species from the southeastern Edwards Plateau and *E. rathbuni* is not part of this clade

Wiens et al. 2003
Revell et al. (2007)

- Two questions to examine adaptive evolution:
  - Are the taxa more similar to each other than to more closely related species?
  - Did the similarity evolve with the shared selective regime (convergence) or prior to shared selective regime (exaptation)?
- Proposes a statistical approach to examine evolution of a convergent feature
  - Uses a fully resolve phylogeny with branch lengths proportional to elapsed time (molecular clock)
  - Principal component analysis on changes in morphological characters

- Case study: rock-dwelling lizards
  - Study species: Five species of rock-dwelling lizards from four families, and non-rock-dwelling species from each family for comparison
  - Examine whether changes associated with transitions to rock-dwelling differ from changes elsewhere on the phylogeny
  - Construct a phylogeny for each study species from mtDNA sequences
    - Estimate branch lengths and divergence times
    - Reconstruct nodes

Revell et al. 2007
• Transition to rock dwelling did not always result in the same changes
  • Most lineages evolved longer limbs and flatter heads
    – *Anolis bartschi* and *Pseudocordylyus capensis* evolved marginally flatter heads
    – *Petrosaurus thalassinus* evolved smaller limbs

• Not all changes occur in parallel
  – Only four of five lineages evolved longer hindlimbs
  – Magnitudes of flat head were small in two lineages

• Two possibilities:
  1. Species interact with environments differently?
     – No evidence for this
  2. **Different ancestral starting points → different evolutionary changes needed to bring species to comparable endpoints?**
     – Maybe!!!

• Conclusion: lineages with different morphologies evolve in parallel and may not produce highly similar outcomes
  – However, there is an evolutionary trend:
• Not all changes occur in parallel
  – Only four of five lineages evolved longer hindlimbs
  – Magnitudes of flat head were small in two lineages
• Two possibilities:
  1. Species interact with environments differently?
     – No evidence for this
  2. Different ancestral starting points $\rightarrow$ different evolutionary changes needed to bring species to comparable endpoints?
     – Maybe!!
• Conclusion: lineages with different morphologies evolve in parallel and may not produce highly similar outcomes

Reveill et al. 2007