Two Views of Adaptation

**Adaptation as a process**
- The process by which an organism becomes better fitted to its environment, and stays that way
- Reflects role of natural selection in evolutionary origin of traits that allow animals to meet challenges to survival
- Also reflects role of natural selection in maintenance of traits--accounting for persistence of traits in spite of their costs

**Adaptation as an outcome**
- A trait that has survival value
- Results from natural selection favoring a particular phenotypic design that maximizes some survival or reproductive benefits relative to costs
Challenges in Studying Adaptations as Outcomes of Natural Selection

Deciding whether you need to consider both the historical and the current adaptive function of the trait

- Extreme view: a trait is an adaptation iff (if and only if) natural selection is responsible for both origin and persistence
- Moderate view: a trait is an adaptation if natural selection is responsible for its persistence--its current utility
- Example: prehensile tails of New World Monkeys

Determining whether natural selection actually does play a role in maintaining trait in current populations (going beyond "Just-So Stories")

- Is there variation?
- Is variation heritable?
- Understanding selection pressures that produce differential success
  - Are deviations from the norm penalized, and if so how?
  - Value of experimental studies in creating extreme deviations from norm
  - Value of interspecific comparisons: correlate trait differences with environmental differences

Understanding adaptive value of a trait is a matter of understanding both its benefits and its costs
Levels of Selection

If adaptations evolve and are maintained because of their “survival value,” then whose survival value should we be concerned about?

Species/population/social group?
(Group selection, or differential success of groups showing different variants of trait)
• Generally, will be a weak evolutionary force
• Counteracted by gene flow between groups and individual selection within groups

Individual?
(Individual selection, or differential success of individuals within population)

Gene?
(Genic selection, or differential propagation of alternative alleles coding for different versions of phenotype)
An Actual Example: Clutch Size in Great Tits

Why is clutch size normally around 8-9 eggs (and not larger)?
• For good of group or good of individual?

Experiment: vary clutch size by adding or removing eggs

Result: if clutch size is increased, individuals suffer--they are holding back for their own good

Individual or Genic selection?
• Explanations on individual level can be explained in genic terms
• As we shall see, some traits are disadvantageous for individual, but advantageous for genes
Selfish Genes

Some traits cannot be easily explained in terms of individual benefit:
- Alarm calls in which caller exposes herself to risk of predation
- Helping at the nest: forgoing reproduction and helping others reproduce
- Self-sacrificing defensive behavior (social insects)

Individual suffers cost, but may benefit
- Altruistic behavior is often directed at close relatives
- Hence the behavior promotes the success of copies of the genes responsible for the expression of the altruistic trait
The Problem of Imperfection

Common critique of adaptationist approach to biological traits:

Adaptationists (misguidedly) strive to explain traits as “perfect” or “optimal” solutions to particular problems

Natural selection is indeed an inherently optimizing process

However:

• Adaptation must be constrained by limits on what is biologically possible (big question--how do we know what is “biologically possible”?)

• Also: there is a variety of reasons why natural selection might not produce the optimum phenotype even if it is biologically possible
Limits to Perfection

Alcock presents five explanations why traits may be “imperfect” (see Table 8.1)

- **H1**: Time lags: trait evolved under different environmental conditions and there hasn’t been time enough for appropriate mutations to arise or for natural selection to change population
- **H2**: Trait develops as maladaptive side-effect of an otherwise adaptive trait (sickle cell)
- **H3**: Gene flow from a different population prevents members of a local population from reaching optimum
- **H4**: Trait is involved in multiple tasks, and hence has multiple functions that may be mutually incompatible (e.g., flippers of sea turtles constrain adaptation for walking)
- **H5**: Other features of organism limit degree to which a given trait can fine-tuned for a particular function (physical properties of bone constrain skeletal design)

**NOTE**: H2, H4, and H5, are really different manifestations of the same basic constraint: tradeoffs among traits that result from organisms being complex, integrated entities in which the parts must work together.
Limits to Perfection

Time Lags: Moths, Flames

Human traits (aggression, warfare, obsesssions with hunting, lawn care)---adaptations to “Environment of Evolutionary Adaptedness”, or EEA?
Summary

• Adaptations are traits that ensure the survival and reproduction of the animals that exhibit them (or the genes that code for the trait)

• Adaptations may not be perfect, especially in changing environment

• Goal in studying adaptations is to understand selection pressures that (may have) shaped the features we observe