In this (short) unit we'll look at the process and some patterns of adaptive change. Chapter 8 focuses on how we test adaptive hypotheses and some of the complexities of adaptive change. Chapter 9 focuses on sexual selection and the patterns it produces.

Notes for this chapter: On your own, read “Behavioral Thermoregulation” (pp. 261-265) and section 8.5 (Phenotypic Plasticity) and answer the study guide questions. Skip section 8.6

**Topic outline:**

I. The adaptationist program
   A. Defining adaptation
      1. As text authors point out, “the explanation of organismal design is one of the triumphs of the theory of evolution by natural selection” — and one of the key activities of evolutionary biologists is exploring the evolutionary histories of organismal traits
      2. Every evolutionary biologist would agree that, if we want to know the full evolutionary history of a trait, we need to determine
         a. historical origin: how the trait arose, for what function
         b. subsequent modification: what changes in structure, function occurred over time, how those changes occurred, and what adaptive benefit (if any) they had
         c. current maintenance: what is the current function of the structure; what (if any) adaptive benefit does it provide?
      3. Some confusion (and possibly argument) can arise over the terms we use to describe the process; specifically, how we choose to define “adaptation” itself
      4. 2 definitions possible; neither is right -- it's more important to be clear about which meaning is intended than to quibble over which words should be used!
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a. Definition #1: defining by current function (most commonly used)
   i. adaptation = any characteristic that increases the fitness of an individual in its current environment – e.g., fish gills are adaptations for exchanging gas in water
   ii. This definition implies that adaptation must occur by natural selection (because the trait must increase fitness)
   iii. Using this definition, the only test required of an adaptive hypothesis = test of current function: if beneficial function exists, it’s an adaptation

b. Definition #2: defining by history (more restrictive, used more by folks explicitly interested in history of traits – this is not the definition used in the text)
   i. adaptation = trait that arose by natural selection for its current function
   ii. note key difference with #1 = traits that have changed function aren’t called adaptations (called pre-adaptations, proto-adaptations, exaptations, etc.)
   iii. e.g., vertebrate gills are pre-adaptations/exaptations for gas exchange because original function was filter feeding
   iv. In this definition, the action of natural selection is explicit
   v. because of its specificity, to call a trait an adaptation under this definition requires testing hypotheses about original function, current function, and mechanisms of change; so much more restrictive
   vi. key advantage of this definition is that it “forces” investigators to think about whole of evolutionary history of a trait, not just its current function

5. Again, neither definition is right or wrong – but it is important to understand which is being used!

B. Because natural selection can be so powerful, and because it’s been demonstrated to result in so many different kinds of adaptations in different organisms, it’s easy to fall into two major “traps” – both of which we’ll address in this chapter

1. accepting adaptive explanations for a trait because they’re plausible, rather than
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because they’ve been rigorously tested

2. “naive adaptationism” (Gould & Lewontin, 1979) -- idea that every
characteristic, no matter how trivial or bizarre, is an adaptation to something
(which then often leads back to trap #1) – note that this problem arises under
both definitions of adaptation

II. Testing adaptive hypotheses (avoiding trap #1!)

A. Experiments

1. experiments are often considered the “most powerful method for testing
hypoth"es"es” because they allow investigators to isolate and test the effects of
individual variables/factors

2. an important drawback is that experiments may not realistically duplicate or take
into account the full complexity of natural environments
a. so findings from experimental studies (especially lab studies) may not apply
to organisms in their natural environments
b. one way around this problem is to do field experiments – but this won’t be
feasible for many kinds of organisms in many kinds of environments

3. Example of experimental study: wing marking and wing waving in tephritid flies

a. background:
   i. Zonosemata vittigera = small fly with distinctive dark bands on wings
   ii. when disturbed, fly holds wings over body and waves them up and down
   iii. display seems to mimic threat displays of jumping spiders (Salticidae)

b. hypotheses:
   i. original: wing-waving is a form of protective (Batesian) mimicry –
      displaying flies are avoided by other potential predators
   ii. alternative: wing-waving is a form of protective mimicry, but only against
      jumping spiders themselves – not against other predators
   iii. important third possibility (of a sort that should always be tested!):
      markings and displays are unrelated to protection from predators

c. experimental procedure (read details):
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i. “create” flies with different combinations of traits: marking + display, marking but no display, display with no marking, no display and no marking

ii. expose experimental flies to jumping spiders and other predators

iii. record responses of jumping spiders, other predators

iv. note that this setup results in different, mutually exclusive predictions for the three hypotheses, making it particularly powerful:

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Zonostrema tata</th>
<th>Zonostre mata</th>
<th>Zonose mata</th>
<th>Housefly with Zonose mata</th>
<th>Housefly untreated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Purpose</td>
<td>has markings + display</td>
<td>control for effect of manipulation</td>
<td>display but no markings</td>
<td>markings but no display</td>
<td>no markings, no waving</td>
</tr>
</tbody>
</table>

Predictions under hypothesis of no mimicry

<table>
<thead>
<tr>
<th></th>
<th>Jumping spider</th>
<th>other predator</th>
<th>Jumping spider</th>
<th>other predator</th>
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<tbody>
<tr>
<td>attack</td>
<td>attack</td>
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Predictions under hypothesis of mimicry deterring other predators

<table>
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<tr>
<th></th>
<th>Jumping spider</th>
<th>other predator</th>
<th>Jumping spider</th>
<th>other predator</th>
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</thead>
<tbody>
<tr>
<td>retreat</td>
<td>retreat</td>
<td>attack</td>
<td>attack</td>
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Predictions under hypothesis of mimicry deterring jumping spiders

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<tr>
<th></th>
<th>Jumping spider</th>
<th>other predator</th>
<th>Jumping spider</th>
<th>other predator</th>
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<td>retreat</td>
<td>attack</td>
<td>attack</td>
<td>attack</td>
</tr>
</tbody>
</table>

d. results:

i. jumping spiders tended to retreat from flies that waved with marked wings, but attacked others

ii. other predators attacked all flies equally

iii. consistent with hypothesis that flies are mimicking their own predators specifically to avoid being eaten by them

4. Important components of experimental designs illustrated by this study:

a. well-defined and effective controls: in this case, controlling for the effect of
surgery independent of the effect of waving, markings
b. standard conditions for all aspects of study (from test arena to definitions of predator responses)
c. randomization:
   i. in this case, predators were exposed to random sequence of test subjects
   ii. this controls for bias that might be introduced if, for example, hungry spiders change their behavior in predictable ways over time
d. replication reduces effects of unusual individuals or circumstances – general rule is that the larger the sample size, the more reliable the results will be (and this is especially true when using statistical tests)

B. Observational studies
1. Observational studies are used when
   a. experimental studies aren’t feasible
   b. experimental studies don’t accurately reflect the full range of conditions that need to be studied (e.g., field conditions)
2. Note that the only difference between experimental and observational studies is that the latter don’t involve direct manipulation of the organism or its environment
   a. the basic procedure of hypothesis testing (hypothesis, predictions, tests, etc.) is the same
   b. if possible, controls are included
   c. characteristics defining a good experiment also apply to observation, to the extent possible
3. Example of observational study: long necks in giraffes
   a. background: giraffes have very long necks that make for some very awkward situations (e.g., drinking) – seems intuitively obvious that long necks must provide some adaptive advantage to counter the apparent disadvantages
   b. hypotheses:
i. original: giraffes have long necks to allow them to forage higher in trees, giving them access to a food resource not used by other animals

ii. alternative: male giraffes with longer necks have a mating advantage over males with shorter necks (sexual selection – this hypothesis was based on the observation that male giraffes use their heads and necks in aggressive fights with each other)

c. tested by deriving specific predictions from each hypothesis and testing those by observing giraffes in their natural environment (read details):

i. predictions and tests from “foraging height” hypothesis:
   a) predictions = during dry season, when food is scarce, giraffes should forage
      i) above the reach of competitors
      ii) near their maximum height
   b) found:
      i) dry season foraging is primarily on low shrubs, not trees
      ii) even when foraging above competitors, prefer to forage at shoulder height (much lower than maximum)

ii. predictions and tests from “mating advantage” hypothesis:
   a) males should have longer, heavier necks than females: yes
   b) males should have heavier, more “armored” skulls than females: yes
   c) general prediction: males with longer, thicker necks, more massive horns, and more heavily armored skulls should have mating advantage over those with shorter necks, smaller horns, etc. due to
      i) advantage during male-male competition
      ii) females choosing them as breeding partners
   d) specific predictions and tests:
      i) males with longer necks, etc., should exhibit social dominance over others: yes – ~ 65% of displacements of bulls from social groups were bull with longer neck etc. displacing bull with shorter
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ii) males with longer necks should be more attractive to females:

yes: 60.7% of bulls with longest necks successfully induced females to urinate for testing whether or not she’s in heat compared to 33.6% of bulls with shortest necks etc.

C. The comparative method

1. Some adaptive hypotheses predict specific correlations among traits, or between specific traits and features of the environment
   a. testing these kinds of predictions requires looking at multiple species
   b. collectively, tests that make comparisons across species are called “the comparative method”
   c. comparisons can be made via observation, experimentation, or both
   d. the comparative method can potentially be very powerful, as it allows investigators to control for the effects of phylogeny – i.e., to distinguish between these general hypotheses:
      i. the trait is an adaptation to specific ecological conditions
      ii. the trait is not adaptive, it’s just “held over” from an ancestor in whom it was adaptive

2. Example: is testes size an adaptation for winning sperm competition?
   a. background:
      i. Among species of Old World fruit bats = flying foxes (Megachiroptera), males vary considerably in testes size relative to body size
      ii. Similar pattern holds in other animals
      iii. flying foxes roost in groups; group size varies among species
   b. hypothesis: large testes are an adaptation for winning sperm competition
      i. “sperm competition” occurs when females mate with multiple males during single estrus cycle: sperm literally compete for access to eggs
      ii. many studies in a variety of animals demonstrate that producing more sperm (larger ejaculates) gives males an advantage – simply by entering
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more sperm into the “race”

c. prediction: relative testes size should increase with group size
   i. females in larger groups should have more opportunities for multiple mating than do females in smaller groups
   ii. so sperm competition should be greatest in larger groups

d. simple test: test for correlation between relative testes size and group size for as many species as possible
   i. found significant positive correlation, supporting the hypothesis

e. problem with simple test: doesn't control for phylogeny
   i. remember that the strength of a test increases with sample size
   ii. remember also that our hypothesis, more explicitly stated, is that “every time a species has evolved larger group size, it has evolved larger relative testis size”
   iii. simple correlation assumes that each species represents an evolutionarily independent sample or “event” – i.e., that group size and relative testes size evolved in each one independently of the others
   iv. if our sample includes clusters of closely related species, then each cluster – not each species – may be the independent sample or “event” (study figure 8.12; diagram at end of notes); i.e., large group size and large testis size may have evolved fewer times than we think based on the number of species
   v. this reduces our sample size and weakens our conclusions

3. Controlling for the effects of phylogeny: phylogenetically independent contrasts
   a. general approach = look at patterns of divergence as groups of species evolve independently from common ancestor
   b. requires that we have a good phylogeny for the group of species we’re studying
   c. basic method (fig 8.13; handout at end of notes):
      i. identify terminal taxa and nodes = hypothetical common ancestors
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ii. identify pairs of species that have diverged from common ancestor: each pair represents one possible case of “evolved different group size”

iii. for each pair, plot a point representing the amount of change in each character = contrast

iv. if contrasts are correlated, then we can conclude that that each time a species evolved a larger group size than its sister species, it also evolved larger relative testis size

d. note that using this technique:
   i. we control for the effect of phylogeny – but we need to know the phylogeny to use this method
   ii. we wind up with fewer sample points than we have species, but those sample points are independent
   iii. we need techniques to “reconstruct” characteristics of the hypothetical ancestors

III. Tradeoffs and constraints

A. One problem with “naive adaptationism” is that it fails to consider that individual traits may not be adaptive in and of themselves – it’s possible that, considered by itself, a trait may actually seem maladaptive, but be the way it is because of
   1. a tradeoff with some other trait/function
   2. an evolutionary constraint

B. Example of an evolutionary tradeoff: female flower size in *Begonia involucrata*
   1. background:
      a. this plant is monoecious: has both male and female flowers on the same plant
      b. flowers are pollinated by bees
      c. male flowers provide “reward” = pollen to bees
      d. female flowers provide no nectar; bees visit because female flowers mimic male flowers (same size, shape, etc.)
      e. bees prefer male to female flowers; this presumably creates selection
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pressure for female flowers to resemble male flowers

2. alternative hypotheses for how selection should act on female flowers (fig. 8.23):
   a. H1: female flowers that most closely resemble male flowers will be visited most often and have highest fitness
      i. selection is stabilizing
      ii. “best” female phenotype is the same as the mean male phenotype
   b. H2: female flowers that most closely resemble the most rewarding male flowers will be visited most often and have highest fitness
      i. if larger male flowers offer bigger rewards (more pollen), then bees will prefer them
      ii. selection will be directional, always favoring larger female flowers over smaller

3. Prediction, test (read details):
   a. If H2 is correct, then given a choice of flower sizes, bees should prefer the largest ones; if H1 is correct, no particular pattern of choice should be apparent
      i. investigators made small, medium, and large artificial flowers
      ii. bees preferred larger flowers
      iii. conclusion: selection on female flowers is directional

4. Problem: if selection is directional, female flowers should be larger than male flowers – but they’re not
   a. new hypothesis: a tradeoff exists that prevents larger female flowers from being selected
   b. prediction: inflorescences with larger female flowers also have fewer flowers
      i. tradeoff due to limits on energy, nutrients
      ii. selection should favor more flowers, as the number of seeds is more a function of flower number than of flower size
   c. tested by measuring number, size of flowers on 74 inflorescences; predictions met
C. Example of evolutionary constraint: flower color change in *Fuschia excorticata*

1. background (fig. 8.24):
   a. bird-pollinated tree from New Zealand with long, bell-shaped flowers; ovary is at the base, below the abscission zone (region where flower falls off once ovules are fertilized)
   b. flowers are initially green, then turn red over after ~ 5.5 days
   c. after ~ 7 days, aren’t producing nectar; after ~ 8 days, stigmas aren’t receptive to pollen
   d. after about 5 days, red flowers drop
   e. pollinators strongly prefer green flowers and virtually ignore red flowers

2. Question: why do the flowers change color?
   a. simple answer: advertise to pollinators not to visit:
      i. this helps the plant because visits to late flowers don’t result in offspring for plant – plant only wants visits to “fertile” flowers
   b. But why don’t plants just drop flowers? it would be more efficient (pollinators couldn’t make “mistakes”) and would save energy/nutrients

3. Hypothesis 1: red flowers attract pollinators to tree, where they then visit and pollinate green flowers
   a. prediction: green flowers surrounded by red flowers receive more visits than green flowers without red flowers
   b. Delph and Lively tested by removing red flowers from some trees and not others, and removing red flowers from some branches and not others: found no difference in pollen deposited on the green flowers in any of the treatments

4. Hypothesis 2: flowers must be retained until pollen tubes deliver pollen to ovary (and styles are very long) – color change is necessary because can’t drop flowers without losing the pollen (constraint)
   a. prediction: the time needed for pollen tubes to grow to ovary should be ~ same as time from color change to abscission (i.e., flower drops as soon as
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possible after pollination)

b. tested by examining ovaries from flowers at different times after pollination
   i. found that after 3 days, 100% of pollinated flowers had pollen tubes in ovaries
   ii. takes at least 1.5 days for abscission to happen once abscission layer begins to grow
   iii. so abscission does happen ~ as soon after pollination as possible while still giving pollen tubes time to deliver pollen to ovary

5. So – why do flowers change color? Because flowers have to stay on tree for some time after they’re pollinated; plants benefit from “warning” pollinators that flowers aren’t “worth” visiting

IV. Summary/conclusions

A. Reconstructing evolutionary histories of traits is a key activity of evolutionary biology
   1. the history of a trait includes its origin, subsequent modification, and current maintenance
   2. biologists may differ on how they apply the term “adaptation” to a trait – some use a historically restrictive definition while others focus on current function

B. Regardless of the definition used, the statement that a given trait is “an adaptation for” some function is a hypothesis that must be tested, not just accepted

C. An array of techniques, including experiments, observations, and the comparative method are used to test adaptive hypotheses – and the underlying procedures and principles are the same used to test any type of scientific hypothesis

D. An individual trait is likely to be the product of complex factors that may include
   1. selection for a particular function
   2. tradeoffs among functions
   3. constraints imposed by other features of the organism’s biology
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Phylogenetically independent contrasts