Now we're going to turn our attention to ultimate questions about behavior. In this chapter, we'll introduce some basic principles of historical analysis through a set of case studies that, taken together, illustrate five major points:

1. Ultimate questions about behavior fall into two broad categories:
    a. Questions about the historical sequence of events leading to the current trait – these are questions about the pattern of evolutionary change
    b. Questions about the causal mechanisms that brought about that historical sequence of events – these are questions about the processes involved in evolutionary change.
2. The comparative method can be used to develop and test hypotheses about both patterns and processes of evolutionary change.
3. Complex traits (behavioral or otherwise) arise in steps. When we're evaluating competing hypotheses about their evolution, parsimony dictates that the hypothesis minimizing the # of steps is the most likely.
4. Traits can shift function over time; the original function may or may not be the current function.
5. Evolutionary change is constrained by existing traits (themselves the result of a lineage's evolutionary history) – different sets of traits have different likelihoods of arising in different lineages

CHAPTER 7: THE EVOLUTION OF COMMUNICATION – HISTORICAL PATHWAYS

A. The evolution of the pseudopenis in female spotted hyenas (Crocuta crocuta) illustrates a number of important principles of historical analysis of behavior.
    1. Description/natural history
        a. Taxonomically, belong to order Carnivora, family Hyaenidae (with four genera, four species)
        b. Spotted hyenas are social carnivores, live in female-dominated packs
        c. Female spotted hyenas have an erectile pseudopenis; when two females meet each other, they engage in an anogenital "sniffing ritual" (much like male domestic dogs).

   d. So, in this context, we can think of the pseudopenis + ritual as a communications signal

2. General question #1: what is the history of the signal? Use a range of information and approaches to try to answer . . .
   a. Look at the species' relatives: did spotted hyenas inherit the pseudopenis and ritual from a common ancestor?
      i. pseudopenis is found only in this species – so seems to have originated with this species
      ii. Anogenital sniffing is widespread within the order – it's reasonable to assume that this component of the behavior was inherited from an ancestor
   b. Look at the anatomical/physiological components of the trait to help narrow the question:
      i. The pseudopenis is actually an enlarged clitoris
      ii. So part of the question can be more specifically stated: how did the clitoris become modified?
   c. Develop a hypothesis based on current knowledge of the trait itself and comparable structures in other species:
      i. We know, from a number of studies, that female spotted hyenas have very high levels of circulating androgens (including testosterone)
      ii. We also know that, in a number of mammals, increasing maternal testosterone levels will cause female offspring to be born with enlarged clitorises
      iii. So, hypothesis = one key component to the evolution of the pseudopenis was increasing levels of maternal androgens during fetal development
      iv. How could we test this further?
3. General question #2: is the signal adaptive? This is a complex question to answer.
   a. This is actually a question about the evolutionary processes responsible for the production, modification, and maintenance of the trait:
      i. Because the term is used differently by different authors, it's very important to

specify what is meant by the phrase "is the trait adaptive":

A. to some, a trait is only considered adaptive it was shaped by selection for its current function

B. to others, any trait that has current adaptive value is adaptive, regardless of what its original function was

ii. Regardless of the specific definition used, if a trait is/was adaptive at any point in its history, it was shaped (at least in part) by natural selection.

iii. So, if we can demonstrate that the trait is or was adaptive, we can conclude that selection was at least one of the processes that produced it

b. For the trait to be adaptive, it must confer a reproductive advantage – do we have any evidence that this is the case?

i. Yes – indirect, but strong: Some 10-20% of females die trying to give birth through the pseudopenis (which encompasses the vagina).

ii. So, for the trait to have persisted over time, there must be some reproductive advantage that, at a minimum, compensates for this mortality.

c. What is the adaptive function of the trait – i.e., how does it confer a reproductive advantage?

i. Two general possibilities here:

A. The pseudopenis is itself adaptive – having it confers a direct advantage on females.

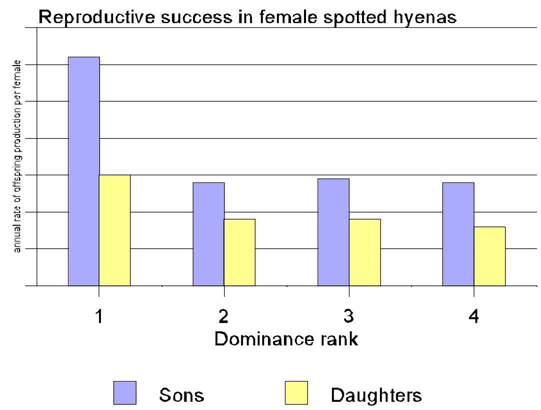
B. The pseudopenis is a neutral (or slightly maladaptive) side effect of some other trait – and it's the other trait that is actually adaptive

ii Adaptive trait may be the androgens that produce the pseudopenis: two hypotheses have been proposed (not mutually exclusive):

A. The androgens make the pups more aggressive (to the point of siblicide). Odd as it may sound, this can actually be an adaptive strategy, especially in environments with unpredictable levels of food resources.

b. The androgens make adult females more aggressive – this would be adaptive because hyena social systems are female dominated

1. Dominance relationships determined by aggressiveness
2. alpha female and her offspring receive more food, especially when food is scarce
3. Alpha females have much higher reproductive success than do subordinate females



iii Two general possibilities aren't mutually exclusive – even if selection originally favored increased androgen levels for one (or both) of the above reasons, it's still possible that the pseudopenis, originally a side-effect, could be "co-opted" for an additional adaptive function

a. in fact, this is likely – the pseudopenis is anatomically and functionally more complex than would be produced solely by an increase in androgen levels
b. suggests continued modification over time – and selection is the most likely process

d. What could the adaptive benefit of the pseudopenis be? Use current function as a guide:

i. current function is clearly some sort of communications signal among females – what advantage could "signalers" and "receivers" get from this?

ii. observational evidence suggests that a consequence of the "greeting ritual" is cooperative behavior among individual females

iii. hypothesis: pseudopenis is a medium for communicating social status – anogenital sniffing of the structure allows females to assess dominance via, e.g., assessing hormonal status

a. benefit to dominant individuals would be decreased cost of aggressive behavior toward subordinates (don't need to fight to maintain dominance against them)

b. benefit to subordinate females would be reduced risk of facing aggression from dominants

iv test the hypothesis:

a. test #1: predict that, because males not involved in the female dominance hierarchy, shouldn't participate in this greeting ritual – confirmed.

b. test #2: predict that, in other female mammals, anogenital sniffing conveys information about hormonal status – confirmed in naked mole rats

4. General conclusions:

a. about spotted hyenas: summarize current thinking =

i. originally, selection favored females with increased circulating androgen levels – this was advantageous because

a) it increased aggressiveness among pups and/or

b) it increased aggressiveness among females

ii. a side-effect of increased androgen levels was the enlargement of the clitoris; this then was co-opted for a signaling function among females

iii. selection favored increased modification of the enlarged clitoris into the pseudopenis we see currently – probably to enhance its signaling function.

b. about addressing ultimate questions:

i. understanding current natural history is critically important

ii. making comparisons among species helps us develop and test hypotheses about the evolution of behavior (and other traits)

B. The evolution of the "rapid-fluttering wing-waving" display in the pelagic shag (was pelagic cormorant) demonstrates use of the comparative method to reconstruct the historical development of behavior (and other traits)

1. Any time we consider the historical development of a complex trait, we begin with the assumption (based on our understanding of evolutionary processes) that the development of the trait involved an incremental series of small changes

(=**cumulative selection**)

2. Try to identify possible stages by examining relatives:
   A. analagous to reconstructing stages of mitosis from individual cells in different stages of the process or reconstructing the evolution of anatomical features by examining fossils at different stages
   B. begin with the simplest available behavior and build hypothetical sequence that minimizes (because of **parsimony principle**)
      I. the magnitude of changes from one step to the next
      II. reversals from a "more advanced" state to a "more primitive" state
      III. the total number of steps from "start" to "finish"
   C. note that this is only going to work for species belonging to reasonably diverse lineages exhibiting a fair amount of variation in the trait in question!
3. Test the hypothesis by comparing hypothesized sequence to known patterns of evolutionary relationship:
   A. test is based on the assumption that the species most alike behaviorally will be most closely related evolutionarily – so that reconstructing the historical sequence of changes will also reconstruct evolutionary relationships
   B. display the hypothesis in the form of a cladogram (= type of evolutionary branching diagram that illustrates evolutionary relationships) that shows when each change is hypothesized to have taken place (note: this is not, as Alcock writes in the legend for figure 4, a matter of deducing the evolutionary sequence from the cladogram!)
   C. compare that cladogram to one derived independently from other characteristics (in this case, DNA data)
   D. predict: if hypothesis is correct, pattern of relationships inferred from hypothesized behavior changes will match relationships inferred from other character sets
   E. in this case, the hypothesis well supported.
4. Some important notes:

A. Clearly, this kind of test requires good understanding of evolutionary relationships –
    I. remember that the "independent cladogram" is itself a hypothesis about evolutionary relationships
    II. if that hypothesis isn't well supported (and we still lack lots of good systematic data for lots and lots of species), then our test isn't very strong.
B. The assumption of parsimony is just that. Sometimes it will be violated (sometimes evolutionary processes *are* complex, reversals happen, etc.)
C. In this case study, we inferred our hypothesis by piecing together stages illustrated by relatives and tested that hypothesis against hypothesized evolutionary relationships. We can also take a different approach: if we have a strong hypothesis about patterns of relationship, we can map the behavioral characters onto the cladogram and use that pattern to develop our hypothesis – this is deducing the evolutionary sequence from the cladogram.
D. either way, we're combining information from current variation in the trait among relatives with information about evolutionary relationships to develop and test hypotheses about evolutionary sequences.
E. Note also that this is another example of a trait (wing-flapping) arising for one function, but then being co-opted for another – wings certainly didn't evolve originally as mating display structures!

5. On your own, read the section on the evolution of signal reception in male whistling moths; think about the effect of the evolution of specific sensory abilities on the subsequent evolution of signals

C. Studies of sensory exploitation demonstrate that the evolutionary history of a lineage biases and constrains future evolution
    1. **Sensory exploitation**
        A. can be defined in general terms as the biasing effect of existing perceptual mechanisms on the origins of communications systems
        B. refers, more specifically, to the hypothesis that a given signal arose evolutionarily

after sensitivity to/preference for that signal arose

C. is a very important mechanism for the evolution of female mate choice in sexual selection – we'll talk more about that later

2. Hypothesis was originally developed by Mike Ryan and colleagues as they studied tungara frogs (Physalaemus pustulosus)
   A. natural history:
      I. males use calls to attract females
      II. calls consist of a "whine" that may or may not be followed by a "chuck"
      III. males that use both chucks and whines are more susceptible to predators
      IV. but, females prefer whine + chuck to either signal alone
   B. Ryan and colleagues studied physiological basis for the female preference and found that
      I. auditory system includes two sets of receptors
      II. each set of receptors is maximally sensitive to different frequency of sound – one to the frequency range of the whine, one to the range of the chuck
   C. hypothesized that the sensory system of females predisposes them to prefer whine + chuck because it provides a greater sensory stimulus than does either signal alone – i.e., that preference for two-part call precedes, evolutionarily, the development of the two-part call
   D. tested the hypothesis:
      I. predict that females will respond favorably to any signal that stimulates both sets of auditory receptors – test by using artificial calls with white noise substituted for chuck – confirmed (fig 18 p. 244)
      II. predict that, if preference is a function of sensory apparatus, females of related species whose males don't produce two-part call should also prefer two-part call – confirmed
   E. Read Basolo's work on sword-tails on your own
3. Another good example = mate signaling in water mites (Neumania papillator)
   A. natural history:

I. both sexes are blind
II. female uses a characteristic “net stance” used to wait for prey
III. when male approaches, he vibrates forelegs in front of female
IV. she grabs male using same response as used for grabbing prey, but releases
V. male then turns and deposits spermatophores in front of female

B. Heather Proctor hypothesized that males were mimicking copepod prey – “exploiting” pre-existing female sensory system originally adapted for prey capture
C. tests:
   I. if male behavior exploits specifically prey detection system, then predict:
      A. copepods should produce same range of vibrations as males – met
      B. hungry females should be more responsive than well-fed females – met
   II. if this is a true example of exploitation, then predict that
      A. “trembling” will only be found in species with female “net stance” (can we legitimately predict that, whenever net stance is found, trembling should be found? why or why not?) – met
      B. trembling should follow, evolutionarily, after development of net stance
         1) Test by mapping both behaviors onto cladogram of this species and relatives
         2) Pattern should be consistent with parsimonious hypothesis of net evolving first, followed by trembling
         3) Result (fig 15 p. 241) = two equally parsimonious scenarios, each consistent with hypothesis that “net stance” arose before trembling.

D. The maintenance of sexual reproduction in parthenogenetic lizards demonstrates the usefulness of “quirky” traits for understanding historical sequences
   1. S. J. Gould uses the term “**the panda principle**” to describe the general principle that, because natural selection is a sequential process that builds on existing traits (vs. designing from scratch), organisms have all kinds of “imperfections:
   2. Those “imperfections” reveal important information about animal’s evolutionary

history

A. e.g., panda's thumb, snake and whale legs, etc. (for anatomical traits)
B. e.g., sexual behavior in parthenogenetic lizards (genus Cnemidophorous)
    I. some species entirely female, producing female offspring asexually
    II. but still engage in sexual behavior very similar to that of close relatives
    III. female fecundity is tied to this behavior – females that are courted and mounted are more likely to clutch than females that aren't
    IV. most parsimonious explanation is that this species descended from sexual ancestors.