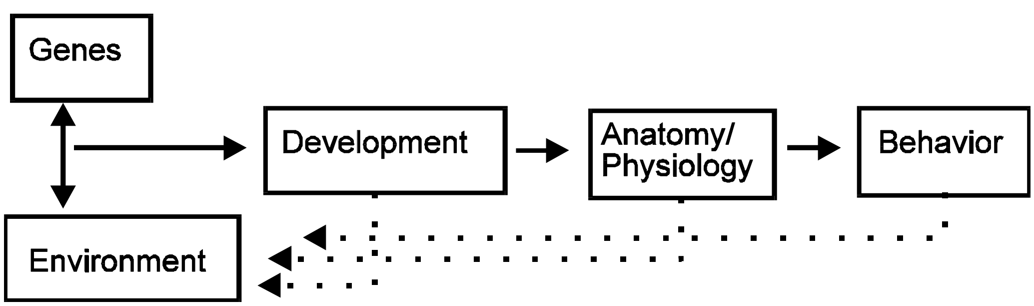
In this chapter, we'll get an overview of how proximate questions about animal behavior are asked and answered, using specific case studies of communication as examples. Then, in chapters 3, 4 and 6, we'll look at the topics introduced in this chapter in more detail.

CHAPTER 2: THE PROXIMATE CAUSES OF BEHAVIOR

A. General introduction:
   1. The proximate mechanisms or causes of behavior consist of two complementary components:
      a. genetic-developmental systems
      b. physiological systems
   2. The underlying model for proximate analysis describes the general relationships among genes, environmental influences, developmental processes, anatomy/physiology, and behavior:



      a. Genes and the environment interact in complex ways to produce/direct developmental processes
      b. Developmental processes produce the anatomical/physiological systems responsible for the production of behavior
      c. Interactions among components persist and change over entire lifetime of animal (dotted arrows) -- we're simplifying by focusing on "straight line" interactions for now

c. NOTE: ALL BEHAVIOR HAS BOTH GENETIC AND ENVIRONMENTAL COMPONENTS, if only because the interaction between genes and environment during development (and the influence is generally more extensive than that)
   i. phrases “the behavior is genetic” or “the behavior is environmental” are inappropriate
   ii. what is appropriate -- and interesting -- is to ask to what extent DIFFERENCES in genes and/or DIFFERENCES in environment produce DIFFERENCES in behavior among individuals or groups

3. Given the above model, we can often begin the analysis of genetic/developmental causes of behavior by formulating two “extreme” hypotheses:
   a. Hypotheses are
      i. differences in the behavior among individuals (or groups) is a consequence of genetic differences
      ii. differences in the behavior among individuals (or groups) is a consequence of environmental differences
   b. Then, to test, the obvious procedure is:
      i. genetically identical individuals/groups in different environments
      ii. genetically distinct individuals/groups in same environments
   c. In real life, this can often be extremely difficult even in lab settings; it’s generally going to be even more difficult in natural (field) settings

B. Studying genetic/developmental causes of behavior
   1. Differences in song/calls between galahs and pink cockatoos in Australia
      a. two species in same genus, same environment
      b. three types of call, all different between species: begging call, alarm call, contact call
      c. occassionally, because of the way they nest, galahs will be reared by

cockatoos -- so perfect way to test the hypotheses about species differences

d. findings: (OH/HO): galahs raised by pink cockatoos exhibit:
   i. galah begging and alarm calls
   ii. cockatoo contact calls
   iii. conclusion: differences in alarm and begging calls is largely genetic; differences in contact calls are largely environmental
   iv. NOTE: this DOESN'T mean that "contact calls are environmental" while "begging calls are genetic!"
e. Note that testing hypotheses about genetic/developmental causes can provide interesting information about physiological causes:
   i. the fact that fostered galahs learn cockatoo contact calls suggests that the auditory/social experiences can affect the gene/environment interactions underlying at least one component of the call systems (the contact call)
   ii. suggests that galah nevous system includes system for perceiving calls of others, comparing to own calls, and modifying own calls
   iii. interestingly, study of zebra finch brains demonstrate that, at least in that species, the acoustic environment directly affects the activity of individual genes acting in the specific part of the brain associated with song control (color plate 1).

2. Interspecific differences in "song" (patterns of wing vibration) in fruit flies -- because of their use as genetic models, we have tons of information about both the genetics and mating/breeding behavior in these flies
   a. Two species (D. melanogaster, D. simulans) differ in two "song" characteristics: IPI and IPI period
   b. In both species, individuals vary in their activity patterns based on their alleles of a specific period gene (per):
      i. wildtype individuals = per^+ have normal (~24 hour) activity pattern

ii. homozygous *per*^{0} are arrhythmic (no apparent activity pattern)

iii. *per*^{s} flie have short patterns; *per*^{L} flies have longer patterns

c. in both species, differences in *per* alleles are correlated with differences in male songs (this is an example of **pleiotropy**: one gene has multiple effects)

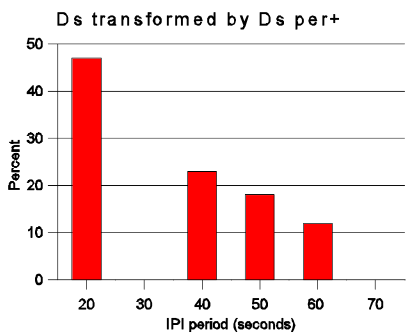
d. Wildtype *per* alleles are different in each species (i.e., D. melanogaster wildtype is different from D. simulans wildtype)

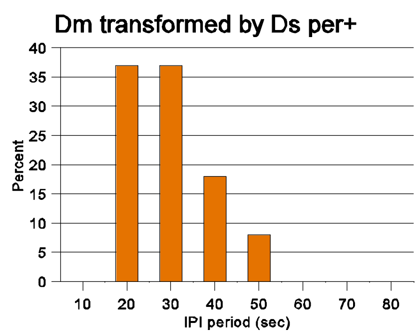
e. **hypothesis**: interspecific differences in song are caused by differences in the *per* allele

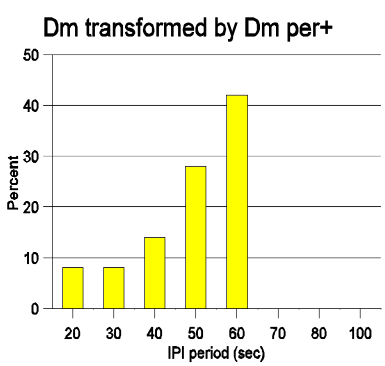
f. Predictions & tests:

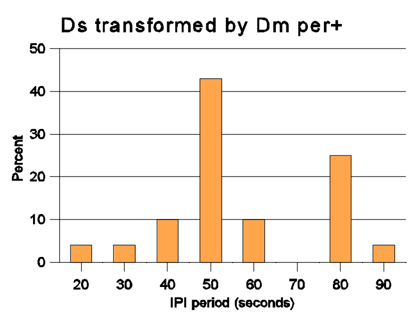
i. male *per*^{0} D. melanogaster transformed by ("injected with") wildtype D. simulans will perform D. simulans "song", and vice-versa

ii. results: meet the predictions: hypothesis confirmed









g. Note that this is particularly unique model system: unlikely to be able to do this with most kinds of behaviors and/or organisms!

3. Differences in song between male and female zebra finches demonstrate the complex interactions between genes, environment, and development:
    a. Males and females are chromosomally (hence genetically) distinct
    b. Genetic differences give rise to key developmental difference between species:
        i. females produce ovaries; pre-ovarian cells do not generate estrogen
        ii. males produce testes; pre-testicular cells generate estrogen, which can then be converted to other androgens in other parts of the body
    c. Difference in hormone levels = differences in the chemical environments of other cells, especially those of the nervous sytem
    d. Hormonal environment has cascading effects on
        i. the development of the **song system** (network of neural elements funning from front of brain -->spinal cord -->syrinx):
            a) the presence of estrogen early after hatching is necessary for the development and maintenance of the song system in males
            b) its absence in females leads to degeneration of the system by selective cell death
        ii. the activation of the song system at maturity = production of male courtship song
            a) requires production of testosterone
            b) so even females with masculinized brains (via estrogen implants) won't initiate courtship song without exogenous testosterone
    e. So, differences in song between males and females are
        i. a function of differences in genes, in the sense that it's the genetic differences that give rise to the initial differences in hormone production
        ii. a function of differences in the internal chemical environment, in the sense that it's the differences in chemical environment that cause the differences in adult anatomy/physiology

C. Studies of song learning illustrate complex interactions between genes, environment, and physiology in production of behavior

1. Male White-crowned sparrows sing different songs depending on location (song dialects) (play) -- why?
   a. Test hypothesis that differences in song are due to genetic differences:
      i. rear nestlings from two areas in isolation in the lab; if song differences are genetic, each will sing “own” song
      ii. results: males reared in isolation never develop full courtship song at all!
      iii. conclusion: song differences may have genetic component, but the behavior obviously has a more complex basis than original hypothesis suggests
   b. Test hypothesis that differences in song are due to environmental differences: specifically, differences in songs produced by adult males while nestling is developing
      i. male nestlings raised with “tutor tapes” of adult males develop the song of their tutor, regardless of the nestlings’ or the tutor’s area of origin
      ii. strongly supports “environmental difference” hypothesis: nestlings match their own developing song to those they hear as they develop
   c. Genetic & physiological component indicated by clear constraints on song-learning ability in birds reared in isolation:
      i. ability to learn is limited to dialects of white-crowned sparrow song -- birds reared in isolation will not learn songs of other species
      ii. “tutor” songs must be heard during **critical learning period** of 10-50 days after hatching; later than that, normal full song doesn’t develop
      iii. during subsong phase (150-200 days after hatching), nestlings must be able to hear themselves sing (to match their song to that of their tutors)
   d. Social experience also plays an important role:
      i. white-crowned sparrows reared in cages near living adults of other

species learn “social tutor”’s song even though white-crowned tapes also present

ii. white-crowns older than 50 days can still learn “alien” song, even though they first hear it after the critical learning period

2. Putting it all together: what are the proximate mechanisms responsible for differences in dialects?
   a. environmental differences in sounds heard from other singing males lead to differences in song development
   b. those differences have their effects because of specific attributes of neural systems (physiology)
      i. batteries of nerve cells “record” information from neighboring birds
      ii. neural system follows hierarchical “decision-making tree”:
         a) if visual + vocal cue present, follow visual cue
         b) if only vocal cues are present, follow own species
      iii. acoustic/brain systems allow individual to match developing song to “recorded” song
3. On your own -- read about song development in brown-headed cowbirds