Chapter 2
Proximate and ultimate causes of behavior
(2nd Lecture)
Why do extant white-crowned sparrows have a nervous system that enables them to develop a song that is distinct from that of any other extant sparrow species?

There are 2 general types of hypotheses that one could propose to answer this question:

**Adaptationist:** postulates that the attribute evolved through natural selection; attempts to identify the adaptive (reproductive) value of the attribute

**Nonadaptationist:** postulates that the attribute arose incidentally by chance; assumes that the attribute does not impact fitness of animal
**Adaptationist hypothesis 1**
In the past, male white-crowns with a recognizable and familiar song might have enjoyed a reproductive advantage because they were more “attractive” to females.

**Prediction**
Extant females should prefer the songs of males from their own species.

Indeed, female red-winged black-birds were more likely to make a precopulatory display in response to a recording from a conspecific than heterospecific song.
Adaptationist hypothesis 2
Species that occupy different habitats may evolve different song properties to overcome special environmental obstacles to being heard.

Prediction
Different populations of the same species should evolve songs that transmit optimally in their local habitat.

Spherical spreading of sound in an open field

How would this process change in a densely forested area?
Great tits from dense forests produce pure whistles of relatively low frequency, whereas males that live in more open woodlands use higher sound frequencies in their more complex songs.

Do these data provide support for the adaptationist hypothesis? If so, how could you make these results more persuasive?
**Adaptationist hypothesis 3**
Species differ in mate attracting songs because of the disadvantages of producing hybrids.

**Prediction 1**
The acoustical properties of closely-related species should differ more in areas where the risk of hybridization is greater (i.e., in areas where their ranges overlap) than in areas where only 1 species occurs.

Results from a study with 2 species of tree frog.
Adaptationist hypothesis 3
Species differ in mate attracting songs because of the disadvantages of producing hybrids.

Prediction 2
The songs to two closely-related bird species, which are geographically isolated from one another, should not have diverged greatly.

It turns out that both species have divergent songs.

How could you reconcile these results with the adaptationist hypothesis?
Why do male birds sing?

**Mate attraction hypothesis**
Singing functions to inform conspecific females of its species identity and of its quality as a potential mate.

**Male-male competition hypothesis**
Singing functions to inform other males of an individual’s fighting ability, warning rival males to stay away from an occupied territory of a fertile mate.
**Mate attraction hypothesis**
Singing functions to inform conspecific females of its species identity and of its quality as a potential mate

**Prediction 1**
Males of a monogamous species should sing loudly and constantly before acquiring a mate, but stop singing afterward.

Male great tits essentially cease singing once they acquire a mate (before). If their mate is experimentally removed they begin to sing more often (during). Once their mate is returned to them, they reduce singing once again (after).
**Mate attraction hypothesis**
Singing functions to inform conspecific females of its species identity and of its quality as a potential mate

**Prediction 2**
Females should prefer to mate with the males that appear to be the highest quality potential mates. One measure of quality could be the number of song phrases in a male’s repertoire.

This figure shows the relationship between the speed at which a female pairs with a male and begins to lay eggs and the size of the male’s song repertoire.

Y-axis: # of days from the date that the male claimed a nest box to the date that the female laid the first egg.
Male-male competition hypothesis

Singing functions to inform other males of an individual’s fighting ability, warning rival males to stay away from an occupied territory of a fertile mate

Prediction 1

Rival males should be less likely to enter an established territory if a male is actively singing

In this expmt, resident male white-throated sparrows were experimentally removed from their territories. The results show that the vacant territories attracted fewer intruders when taped song of the removed male was broadcast.
So, what can we conclude? The data support both hypotheses.

**Mate attraction hypothesis**

**Male-male competition hypothesis**

It probably serves both functions.
What is the functional significance of dialect formation in bird song?

Males in each location have their own distinctive song dialect, as revealed in these sonograms of the songs of six birds from each location.
Adaptationist hypothesis
Learning a local dialect enhance a males reproductive success

Prediction
Females should prefer to mate with males that produce the local dialect

Female cowbirds prefer the song of male of their own subspecies.

When females of subspecies A hear the song of males of their own subspecies (A/A), they are much more likely to adopt the precopulatory position than when they hear the songs of males of another subspecies (A/B)
So, why do birds produce different songs?

**Proximate Causes**

- Differences in gene–environment interactions
  - Hormonal differences
  - Differences in song system construction
  - Differences in song system operation

**Ultimate Causes**

- **Song differences among individuals**
  - Species differences in song (which may affect mate choice)
  - Sex differences in song (which may affect mate choice)
  - Dialect and repertoire differences (which may affect territory defense)

- Differences in reproductive success = Natural selection

- **Genes transmitted to the next generation**

- **Differences in gene–environment interactions in individuals**

- **Process repeats itself**