Swamp and Song Sparrows

Dialect variation in white-crowned sparrows

Song dialects
- 12 dialects of the Puget Sound white-crowned sparrow

Dialect variation in bird song
- Learned or inherited?
- Effects of rearing in isolation
- Template matching
- Effects of deafening (auditory feedback)
Stages in song development: white-crowned sparrow

- memorization phase (10-50 days of age)
- subsong phase (150 days of age)
- overproduction phase ("plastic song")
- song crystallization
- full song (200 days of age)
- action-based learning and selective attrition

“The sounds uttered by birds offer in several respects the nearest analogy to language, for all members of the same species utter the same instinctive cries expressive of their emotions; and all the kinds that have the power of singing exert this power instinctively; but the actual song …is learnt from their parents or foster-parents. These sounds … are no more innate than language is in man. The first attempts to sing may be compared to the imperfect endeavour in a child to babble.”

Charles Darwin (1871:i:55)

Stages in song development: white-crowned sparrow

- Memory-based learning – During the memorization phase (10-50 days of age) young male white-crowned sparrows listen passively to species-specific songs without responding.
- Hearing the species-specific song is essential for normal song production in adulthood.

Stages in song development: white-crowned sparrow

- Action-based learning: Later, during the “plastic song” stage (150-200 days) the male bird improvises and produces many variants of the song. Song crystallization involves selective attrition, dropping components of the song that do not match the dialect and/or the song patterns of neighboring birds.

Subsong

- 7-second segment of subsong performed by a 240-day old white-crowned sparrow.

Source: http://blb.biosci.ohio-state.edu/nelson.html
**Subsong**

- Another example of subsong, this one from a swamp sparrow.
- Adult version of the swamp sparrow song.

**Plastic song**

- 9 seconds of plastic song from a 260-day old white-crowned sparrow. The tutor songs were heard and memorized during the sensitive phase.

Source: [http://blb.biosci.ohio-state.edu/nelson.html](http://blb.biosci.ohio-state.edu/nelson.html)

**Song template**

- Young birds deprived of the experience of hearing their species-specific song develop a distorted song (although some aspects of the normal song are present).
- Either tape tutors or live tutors provide the auditory input needed for normal song.

**Song template**

- White-crowned sparrows deafened after the song memorization stage never develop normal song (Konishi, 1965). They must hear themselves sing in order to develop a crystallized version of the song they experienced as nestlings.

**Song template**

- **Conclusion:** Translating the memorized song into a motor program involves ongoing comparison between an internalized template of the song and the auditory feedback from the bird’s own voice.
Neural mechanisms

- Dedicated circuits in the central nervous system, described as the **HVC song pathway**.


Species differences in song development

- **Open-ended learners**: new song patterns are developed beyond the first year.
- Typically, new songs are developed at the beginning of a new nesting season.
  Examples: Canary, Eurasian starling

Auditory feedback

- Early studies showed little effect of deafening in **age-limited** learners once they reach adulthood.
- Later studies showed a different pattern in **open-ended learners**: in canaries, deafened adults show song deficits within a few weeks of losing their hearing.
- **Conclusion**: auditory feedback can help to maintain normal song even after song crystallization.

Species differences in song development

- **Age-limited or sensitive period learners**: Song memorization is limited to the first year of life; no new songs are acquired in adulthood. Examples: Zebra Finch, White-crowned Sparrow.

- **Species differences in song development**: Not all species fit neatly into the two-way distinction between **age-limited** and **open-ended** learners.
- There may be species differences in the dependence on auditory feedback and the degree of song crystallization.
Vocal learning

• One type of information coded in bird song is **individual identity**. Individual recognition depends on learning and long-term memory.
• Recognition of **group identity** (dialect differences) and **species identity** also depend on learning in some species.

Vocal learning

• How widespread is vocal learning in the animal kingdom? How widespread is individual (voice) recognition?
• Best known examples are oscine birds (songbirds) but other groups show individual recognition of offspring and parents (e.g. emperor penguins).

Two voices are better than one

• Voice recognition by mates and offspring in emperor penguins (Current Biol. 10(17), R634-636).

**Question**: How does an adult emperor penguin find its mate and offspring on a featureless ice flow in a crowd of 1000s of penguins packed at densities of 10 per square meter?

**Answer**: they use two voices.

Emperor Penguins

**Why do birds have two voices?**

• Greenwalt (1968) used the term “**two-voice phenomenon**” to describe the ability of birds to produce two sounds, either independently or simultaneously, using the different sides of the **syrinx**.

Songbird syrinx

**Benefits of two voices for recognition**

• Counter-calling + approach strategy
• Calls have rich spectral structure
• Calls are highly stereotyped within individuals but highly variable across individuals
• The two sides of the syrinx produce distinct frequency bands in the penguins’ calls. These bands interact to create **beats**.
Beats and amplitude modulation

- When two sounds have slightly different frequencies, they interact to produce audible beats (rising and falling in amplitude).

Beats provide “signatures”

- When one of the two “voices” was removed from the signal, adults and chicks could no longer recognize the caller. Further testing showed that beats and amplitude modulation were responsible.

Beats improve the long-distance transmission of calls

- The amplitude modulation produced by the “two voices” showed much less degradation with distance than other properties of the calls.

Beats provide “signatures”

- Conclusion: The two-voice phenomenon has an important function (mate/offspring recognition) and an adaptive value (effective long-distance signal propagation in a crowded environment).

African elephants

- Elephants live in close-knit, long-lasting groups and are in constant communication.
- In adult male elephants, testosterone levels are elevated for one month each year.
- During this time they compete aggressively with other males to establish their dominance status and to gain access to females.
- This condition is called musth.

African elephants

- Adult male elephants produce an acrid, penetrating odor from a gland on their faces.
- During musth elephants become very aggressive towards other elephants (and, in captivity, toward humans).
African elephants

- Young male Indian elephants in musth (and possibly African elephants as well) produce a sweet, honey-like scent “like a mixture of flowers.” In India this state is called moda.
- Moda males seem to be broadcasting immaturity and unwillingness to fight for dominance and mates. Older musth males avoid or ignore moda males (and vice versa).

African elephant

- In response to the musth rumble of a high-ranking male, other musth males approached the speaker aggressively, whereas non-musth males walked away from the stimulus.
- The calls of estrous females attracted musth males who approached the speaker rapidly, while non-musth males listened and then walked away.
- Females responded to the musth rumbles of males by approaching the speaker, vocalizing or secreting from the temporal glands.


Elephants

- Kingdom: Animalia
- Phylum: Chordata
- Class: Mammalia
- Order: Proboscidea
- Family: Elephantidae
- Genus: Elephas
- Species: maximus

Asian Elephant

Giraffe Odor

- Older male giraffes are known to transmit a powerful, unpleasant odor, detectable at a large distance.
- Wood (Science, 2002) has discovered that chemicals in the giraffe’s hair contain a range of antibiotics and parasite repellants. Among other things, these compounds stunt the growth of microbes that cause athlete’s foot.
- Giraffe’s scent may also serve a sexual function, perhaps serving as an indicator of resistance to disease and infection.

An Asian Elephant Imitates Human Speech

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Common Raven (Corvus corax)

- Kingdom: Animalia
- Phylum: Chordata
- Class: Aves
- Order: Passeriformes
- Family: Corvidae
- Genus: Corvus
- Species: Corvus corax

Ravens in Maine

  - Ravens have a large repertoire of sounds.  
  - Yelling – sound made by ravens when feeding on the carcass of a moose or deer in winter.  
  - Yelling sounds like a dog whose tail has been caught in a slammed door.

Figure 12.9: Raven yells
Ravens in Maine

- A raven yelling can be heard up to a mile away on a clear winter day.
- Ravens use this call only when they find a rich and scarce food source (carcass of a dead animal, like a moose or deer in winter).
- Yelling attracts other ravens to the carcass.

Ravens in Maine

- Why do ravens yell?
- Why attract competitors when food is scarce?
  - Maybe yelling helps the *group* as a whole (*group selection* account)?
  - Maybe yelling attracts *family* members (*kin selection* account)?
  - Maybe yelling helps the *individual* somehow?

Ravens in Maine

- Ravens yell more when they are hungry.

![Graph showing days without food and number of ravens yelling](image)

Ravens in Maine

- If yelling is directed at family members, then most of the members of the flock should be related.
  - Heinrich found up to 15 ravens at a single carcass, but raven families produce at most six offspring in the breeding season.
  - Later, genetic fingerprinting confirmed that most members of the flock were unrelated individuals.

Ravens in Maine

- Could yelling be directed at *other* predators, like coyotes or bears, who could open the tough-skinned carcass of a dead moose?
  - No: ravens do not always yell when they find a carcass. Sometimes they yell even when the carcass is already ripped open.

Ravens in Maine

- Does yelling “dilute” the risk of predation for an individual bird by attracting others?
  - No, because ravens continue to yell even after the flock has reached its largest size.
Ravens in Maine

• Does yelling provide a benefit for ravens who are not members of the resident, territorial group?
  – Adult ravens maintain year-round territories.
  – Non-resident wanderers (unmated young birds) are driven out by resident, territorial birds
  – Yelling might be a strategy to attract other non-residents to gang up on the residents.

Ravens in Maine

• Gang-up-on-territorial-residents hypothesis
  – Resident territory owners never yell
  – Non-resident, non-territory holders yell
  – Yelling attracts other non-residents to the carcass
  – Residents are unable to drive off non-residents

Ravens in Maine

• Gang-up-on-territorial-residents hypothesis
  – Ravens at a carcass are either (1) a small group of exclusively residents or (2) a large flock of residents + non-residents.

Ravens in Maine

• Mobile roosts as “information centers”
  – Marzluff and Heinrich (1996) reported that ravens form temporary roosts near newly discovered food sources (a large animal carcass).
  – Hypothesis: these mobile roosts serve as “information centers” to provide roost-mates with the opportunity to share their knowledge of food sources.

Ravens in Maine

• Mobile roosts as “information centers”
  – Are the informed ravens leading the group?
  – When captured (naive) ravens were allowed to re-join the group they always followed the others.
  – When captured ravens were given knowledge of new food sources (by releasing them at new carcasses) they joined roosts and sometimes led the others to the food source.
Ravens in Maine

- *Mobile roosts as “information centers”*
  - The same individual would act as a “leader” when provided with knowledge of a new food source, and as a “follower” when it was denied knowledge that other birds in the roost knew.
  - Remaining questions:
    - How do ravens share this information? Vocalizations?
    - How do they decide which individuals have reliable information?