Animal Signalling and Communication

Outline:
1. Purposes and variety of signals
2. Signals in evolutionary context
   - Tactical components
   - Sensory exploitation
   - Unintended receivers
3. Evolutionary thought on signalling
   - Strategic components
   - Honest and deceptive signals
   - Zahavi’s handicap principle
4. Specific examples in territorial behavior
5. Information in groups of foragers
   - Honey-bee example. The “Waggle Dance”
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   - Honey-bee example. The “Waggle Dance”
   - Convergent evolution in “seet” calls
6. Parental care: offspring/parent recognition
   - Studholme (1994): Fiordland penguins
   - Offspring orient to and respond to their parent’s calls more than other calls. (But parents seem less responsive to their particular offspring’s call.)
   - Conveying Hunger levels:
     - Adult birds bringing food back for nestlings. The hungrier nestlings could scream louder.

Purposes of Signals

1. recognition of species, individuals, neighbors, castes (social insects), kin, or demes
   - Bird-song differences between species: are they adaptive?
     - Allopatric Speciation
     - Hybridization zones
     - If hybridization decreases fitness, we’d expect greater song differentiation in areas of closely-related species overlap.
   - Gill and Murray (1972): Compared bird songs of golden-winged and blue-winged warbler in areas of species overlap and non-overlap
     - Songs were less varied in areas of overlap, perhaps because it was adaptive to be more specific.
     - But this is a lone study amongst many that suggest bird song is not so important for species recognition.

2. Sexual ritual or calling behavior between males and females
   - Tungara Frogs
   - Fireflies

3. Establishing territories and/or social status
   - Red deer, red-winged blackbirds

4. Alarm calling
   - Ground squirrels
   - Great tits and other birds subject to raptor predation
   - Convergent evolution in “seet” calls

Signal Components

Tactical Components:
Features of a signal which are concerned with how easy it is for the signaller to transmit it, for the receiver to receive it and discriminate it from other signals.

Strategic Components:
Properties of a signal that are concerned with what good they do to the signaller, i.e. how does the signaller benefit from emitting the signal.

Both have been viewed from an adaptationist perspective.

Tactical Components
“Getting the message across”

Example from Johnstone (1997): Anoline lizards and the “assertion display” versus the “challenge display”

The assertion display is not sent out to anyone in particular. But it “ought” to be noticed by some other lizard.

- Common features of signals ensuring their appropriate reception:
  1. Conspicuousness
  2. Stereotypy
  3. Redundancy
     - Analogy to electronic signal transmission
  4. Alerting components
Tactical Components and the Environment

Signals’ conspicuousness seems to have evolved with respect to the environmental background.

  - Rated sonograms of birdsongs for period of repeat of elements
  - buzzes
  - side-bands
  - Categories for habitat type (i.e. grassland versus forest, etc)
  - Songs from birds in open habitat had more reverberation-degradable features than songs from forest habitats.

Some Sonograms of different birdsongs

The Comparative Method

• Definition:
  - Quite often, the relationship between two traits, or the relationship between an environmental characteristic and an organismal trait will be explored by comparison of the traits and environments across species (or other taxa).
  - The goal is to demonstrate a significant correlation between the two traits in question, or between the environmental conditions and the trait. This, then, might be taken as evidence of adaptation. This process is called the Comparative Method.

• Example:
  - Studying, for example, the length of a repeated element in bird songs versus the amount of reverberation from the environment

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Env. Reverb

The Nasty Statistical Issue:

- It is important to know if the observed relationship between the two variables in statistically significant. However a simple linear regression (put a least-squares-fit line through the data and then test to see if the slope of the line is significantly different from zero) is invalid because it assumes that all the observations are independent.

But in the comparative method, the different points are not independent. They are related by their common phylogenetic history. Consider:

Tactical Components and the “Audience”

“Color blind organisms should not have colorful displays or signals.”

Sensory Exploitation:

When signalling behavior evolves to take advantage of pre-existing sensory biases.

- Proctor (1991): Male water mites “tremble” at a similar frequency to prey. The females are acutely sensitive to this (being part of their foraging behavior repertoire).

The female grabs at the male who somehow contends with the female’s mouth parts, and is able to effectively mate with her.

Was this sensory exploitation? (Proctor 1992) and phylogenies.

Tactical Components and Unintended Audiences

Any time an animal is signalling, the message may get picked up by an unintended receiver (for example a predator).

Two types of alarm calls in great tits:

- Mobbing alarm call: loud indiscreet signal to others to mob and molest a perched hawk.

- “Seet” alarm call: short, high-pitched, discrete alarm call given to warn others of a flying hawk.

The frequency of the seet call is high enough that hawks cannot hear it very well, but it is well within the range that great tits can hear well.

(Studies with hawk orientation to recorded seet calls.)
The Evolution of Strategic Components of Signals

Traditional Ethological View (Pre-1970’s)

• Signals were there to “facilitate and coordinate social interactions by making information available to be shared.”
• Reasonable for cooperative signaling---
  • When both the signaller and the receiver benefit
• Deceit was not commonly considered, even though it was well-known on an inter-specific level, i.e. Batesian mimicry:
  - Viceroy Butterfly
    *Basilarchia archipus*
  - Monarch Butterfly
    *Danaus plexipus*

Signalling and Conflict of Interest

Early 1970’s. Maynard Smith and game theory for signalling---without appropriate controls deceit should abound and signals should evolve to become meaningless.

Since signals are not all meaningless, something has maintained their honesty or utility. What? Two main (and related) types of explanation:

• "Honest Signals"
• Handicap Principle

These reflect other evolutionary pressures that may be acting on signalling behavior

Honest Signals

An honest signal is one which reflects the true state of the sender by virtue of physical necessity

Examples:

Hill and Montgomerie (1994): Correlation between coloration and nutritional condition of male house finches

Clutton-Brock and red deer roaring contests

Main point = direct link between the ability to generate the signal and the physical condition or foraging ability (taken to be a surrogate for fitness) of the signaller

Handicap Principle

Another way (in theory) to curtail deceit

(Zahavi 1975 and later)

• Similar to the Honest Signal notion, but here the link between condition and the ability to generate the signal is not so clear.
• Rather, deceit is discouraged because one must have high fitness in order to overcome the handicap of the signal.
  • Females have a preference for males with long tails
  • The tails don’t confer a fitness advantage to the males--if anything they are a handicap.

Male Widowbird

Notion of the handicap principle echoes Veblen (1899): *The Theory of the Leisure Class*, and his idea of conspicuous consumption

At the heart of the Handicap Principle are

Condition-Dependent Cost or Benefits

The signal/handicap must cost more for the “low-quality” individual than the “high-quality” individual

Conceptually/Graphically:

This has made actual testing of the Handicap Principle very difficult. Almost no studies have managed to quantify condition-dependent costs.