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

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

5. Information in groups of foragers
   - Honey-bee example. The "Waggle Dance"
   - Number of waggles gives info re: distance to food
   - Direction of the straight-run gives info regarding the direction toward a food source.


Fig 1. The Waggle Dance

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.

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

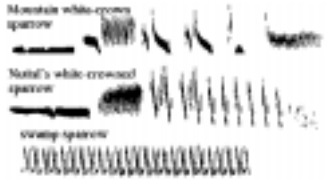
Tactical Components and the Environment

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

•Marchetti (1993): Plumage patterns of congeneric warblers. Those living in low light environments had brighter plumage.

•Wiley (1991): Comparison of song-birds in North American habitats.

- •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 reveberation-degradable features than songs from forest habitats.



Some Sonograms of different birdsongs

Back to the Methodology Zone for a moment:

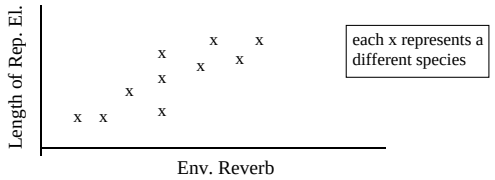
The Comparative Method

•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:

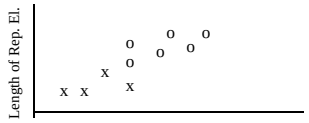
Studying, for example, the length of a repeated element in bird songs versus the amount of reverberation from the environment

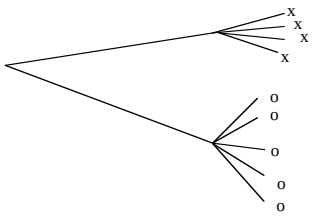


The Nasty Statistical Issue:

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:





If the X's and O's are more closely related to one another, evolutionarily, then the observations in the cluster of X's and the cluster of O's are not independent of one another.

A simple linear regression will treat each point (species) as if it were an independent observation.

The Result: too much statistical significance inferred.

In reality, bird species of the "x" cluster may have all inherited a mutation that shortens the length of song elements, and they may live in less reverberative environments, but the two may not be related.

There are methods to try to correct for the non-independence between closely related species (for example Felsenstein (1985)).

These are what Johnstone is referring to when he uses phrases like "incorporating various measures to control fro the effects of phylogeny."

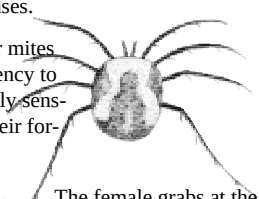
Tactical Components and the "Audience"

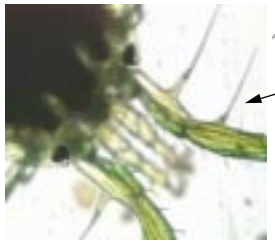
"Color blind organisms should not have colorful displays or signals."

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

Signaller and Receiver don't always stand to benefit in the same way

Examples:

Displays of territory owners

In some species males seek matings with as many females as possible while females seek to mate with the "most fit" males

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

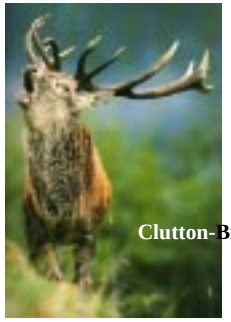
These reflect other evolutionary pressures that may be acting on signalling behavior

Honest Signals

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

Examples:

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



Clutton-Brock and red deer roaring contests

Also, frog-croaking tone. Small frogs are unable to croak at the lowest freqs.

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

Another way (in theory) to curtail deceit

Handicap Principle

(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.
- •Example: Andersson (1982): Male Widowbirds in central africa. The "signal" is the long tail.
  - •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

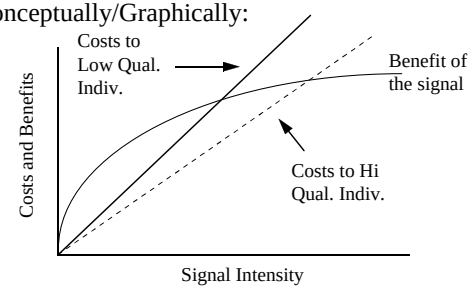
Notion of the handicap principle echoes Veblen (1899): *The Theory of the Leisure Class*, and his idea of "conspicuous consumption"

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.