• **Fixed action pattern**: an innate, highly stereotyped response triggered by a well-defined simple stimulus; once activated, the response is performed in its entirety.

- Egg rolling in geese
  
  Lorenz & Tinbergen (1939)

- Graylag Goose

  http://www.youtube.com/watch?v=vUNZv-ByPkU

• **Imprinting** – form of learning in which individuals exposed to certain key stimuli, usually during an early stage of development, form an association with the object and may later show sexual behavior toward similar objects.

• **Critical period** for learning – a period in the life span of an individual (in birds, a short period just after hatching) where learning or imprinting is greatly facilitated.
Intention Movements

- Ethologists proposed that some communication signals originate from movements made when the animal is getting ready to perform a particular behavior. These movements are called intention movements.
- Examples: bared teeth display in dogs; upright threat posture in herring gulls.

Displacement Behavior

- Ethologists observed that animals may sometimes engage in “irrelevant” activities when they experience conflict. They called these redirected activities displacement behaviors.
- Examples: cat grooms itself when prevented from reaching food; courtship begging in birds.

Ritualization

- Evolutionary process that transforms an incidental cue/behavior pattern into a true communication signal (Tinbergen, 1952).
  - Simplification or reduction in components
  - Exaggeration of the remaining components
  - Repetition of the signal
  - Stereotypy – reduction in the signal variance
    e.g. courtship feeding in pheasants

Evolution of communication signals

- Natural selection results in genetic change in a population when individuals differ in heritable traits that are correlated with differences in their reproductive success

Principle of antithesis

- Darwin proposed that some communication signals arise (evolve) because animals are divided between conflicting tendencies or impulses (e.g. fear and aggression).
- Darwin’s principle of antithesis states that signals with opposite messages tend to be opposite in form.

Antithesis

- Opposition between two conflicting emotional states (attack vs. flee)
- Displays often show extremes in posture, orientation, extent of feather erection in birds, or fur in mammals
Sign stimuli and releasers

- Male **three-spined sticklebacks** in breeding condition will perform a *zig-zag dance* in the presence of a female, but a different display (head-down threat posture) when approached by another male.

- Tinbergen (1951) showed that the cue evoking the zig-zag courtship display was the swollen belly of the female fish; threat was induced by the red color on the underside of a rival male.

- Tinbergen found that simple (inanimate) fish models were sufficient to trigger the response (even a red post office van driving past the window near the fish tank!)

- **Sign stimuli** adapted for communication are called **releasers**.
  - Specialization for signal production
  - Specialization for signal perception
  - discrimination vs. generalization

- **innate releasing mechanisms** – “lock-and-key” analogy
- **Template and filter** models
- Egg recognition in herring gulls (Baerends)
- Supernormal stimuli

**Code breaking**

- The relationship between the triggering cue and the behavioral response of a FAP can be observed when the behavior is exploited by members of another, parasitic species.
- **Code breaking**: behavior that mimics the triggering component of a FAP to exploit its benefits.
Code breaking

• Examples of code breaking
  – colored gape of cuckoo nestling
  – parasitic rove beetle larva mimic the food-begging behavior of larval ants

Supernormal stimuli
  – preference for giant eggs by Oystercatchers

Supernormal stimuli
  – supernormal begging behavior in brood parasites (European cuckoo, brown-headed cowbirds)

Honesty and communication

• Information conveyed by animal signals can provide information about the environment or the sender’s intentions (future course of action).

Honesty and communication

• Most (but not all) communication signals are “honest” (reliable). Why is this?
  • Zahavi (1975) argued that receivers will not respond (and hence communication will not evolve) if the signal is “dishonest” or unreliable.
Honesty and communication

- **Handicap hypothesis**: some signals, like the peacock’s tail, are costly to produce. Since they are costly, they are more likely to be reliable (and this is why female peacocks prefer them).
  
  Zahavi argued that costly signals are more likely to evolve; he describes these as *handicaps*.

Altruism

- **Altruism** is any form of behavior that provides a *benefit* for another individual at a *cost* to the individual performing the action (self sacrifice).

Reciprocal altruism

- **Reciprocal altruism**: sacrifices made by one individual that benefit another individuals that is later reciprocated, so that both gain in the long run. Requires that the two individuals recognize each other as individuals.

Social Behavior

- Social animals live together in *groups* - this practice may lead them to act or behave in ways that facilitate the survival and reproduction of their close *relatives* as well as themselves.
- Fish traveling in schools
- Birds with helpers at the nest

Kin selection

- **Kin selection** is the process that leads to changes in gene frequencies in the population as a result of reciprocal, mutually beneficial actions among related individuals (and who typically live in social groups)

Individual and group selection

- **Fitness** – the more fit an individual is, the higher his or her chances of surviving and propagating his or her genetic blueprint.
- **Individual lifetime fitness** – reproductive output; product of the animal’s lifespan and number of offspring produced (*fecundity*)
**Inclusive fitness**

- To measure fitness it may be helpful to include close relatives as well as the animal itself.
- **inclusive fitness** is calculated from the frequencies of gene survival among a group of genetically related individuals.

**Individual and group selection**

- **Inclusive fitness** – an individual’s total fitness is based on the number of viable offspring it produces, combined with the number of viable offspring produced by its close genetic relatives. (Dugatkin, p. 18)

**Group selection**

- In the 1960s, population biologists began to consider another possible mechanism, **group selection**, that they postulated might also contribute to genetic change. The idea of group selection is that the group, rather than the individual, is the unit of selection.

**The problem with group selection**

- Behavior that is strictly “for-the-good-of-the-species” (such as lemmings committing suicide to make room for other lemmings) will never emerge if there is an alternative, selfish behavior that does not require self-sacrifice.
- “Suicidal lemmings” would quickly die out in the population, to be replaced by selfish, non-suicidal lemmings.

**Reciprocal altruism**

- Not all cases of cooperation involve relatives
- Cooperation between unrelated individuals can pay off in the long run if unselfish actions are “reciprocated”.
  - Safeguards against “cheaters”?
    - Opportunities for repayment, stable long-term social groups, individual recognition, long-term memory
  - Alarm calling in song birds
  - Cooperative hunting in jackals

**Meerkat**

- **Kingdom:** Animalia
- **Phylum:** Chordata
- **Subphylum:** Vertebrata
- **Class:** Mammalia
- **Order:** Carnivora
- **Family:** Viveridae
- **Genus:** Suricata
- **Species:** suricatta
Meerkats

http://www.youtube.com/watch?v=X_eVEW_Y02o

Selfish sentinels in cooperative mammals
Clutton-Brock, TH, O’Riain MJ, Brotherton PN, Gaynor D, Kansky R, Griffin AS, Manser M. Cambridge University

1. kin selection
2. reciprocal altruism
3. optimal activity

• meerkats (Suricata suricatta) guard from safe sites
• solitary individuals as well as group members spend part of their time on guard
• no regular rotation of guard duty
• provision of food increases contributions to guarding

Level of sentinel activity is linked to benefits

A. R. Ridley, N. J. Raihani & M. B. V. Bell
Experimental evidence that sentinel behaviour is affected by risk.

Meerkats increase sentinel activity when pups are present

Peter Santema, Tim Clutton-Brock
Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups.
Animal Behaviour 85 (2013) 655-661

Nest parasitism

https://www.youtube.com/watch?v=43b6GGHITHU

Rove Beetles

Hairy Rove Beetle

• Kingdom: Animalia
• Phylum: Arthropoda
• Class: Insecta
• Order: Coleoptera
• Family: Staphylinidae
• Genus: Creophilus
• Species: maxillosus
Rove Beetles

- Almost 2,900 species of Rove Beetles are found in North America.
- Only a few species are parasitic; most are predatory, feeding on mites, insects, small worms.
- Some species have been used in forensic entomology to determine post mortem interval.

Rove Beetles

- Some species of Rove Beetles in the subfamily Aleocharinae live in termite and ant colonies.
- The larvae resemble their hosts and mimic their behavior (including chemical signals) allowing them to interact with their hosts.

Sensory systems

- Animal communication signals are received by one or more sensory systems:
  - signal detection (e.g. picking up alarm signals)
  - signal discrimination (e.g. deciding if the sounds made by a courting male belong to the right species)

Sensory systems

- Environmental sources of energy: optical, acoustical, mechanical, chemical, heat, and electrical.
- Goal of sensory analysis: to pick up information about environmental events and objects in order to categorize them as edible, dangerous, interesting, or irrelevant.
- Communication signals must be decoded in order to interpret the intended message correctly.

Sensory specialization

- Example:
  - Bats hear ultrasonic (high-frequency) sounds that lie beyond the range of human hearing (30,000-120,000 cycles/second)
  - This sensitivity helps them interpret the echoes returning from the rapid, high-pitched sound pulses they make while pursuing insect prey (echolocation).

Sensory specialization

- Example:
  - Some birds have an extra color receptor not found in the human visual system; this gives them the ability to detect ultraviolet light radiation.
Example:
- The iridescent plumage of starlings (*Sturnus vulgaris*) contains ultraviolet components. Female starlings prefer males whose feathers reflect these components, compared to males for whom the ultraviolet components have been filtered out.

Sensory specialization

• Example:
  - The duck-billed platypus from Australia has a specialized set of receptors around the perimeter of its bill that is sensitive to electrical fields.
  - They use their electrical sensors to hunt for their prey, freshwater shrimps and other crustaceans found in the murky streams where they live.

Sensory specialization

• Example:
  - The star-nosed mole of eastern north America has a set of finger-like projections around its mouth and nose.
  - These projections are highly-sensitive vibration detectors that help the mole locate prey, earthworms and insect larvae, as it digs through underground tunnels.

Sensory specialization

• Example:
  - Rattlesnakes and other pit vipers have two pit organs that register the heat emitted by their prey, at distances up to several feet.

Sensory specialization

• Example:
  - Snakes also rely on a specialized receptor called the vomeronasal organ (VNO) to detect chemical traces in their environment.
  - Chemical residues from the air are brought into contact with the VNO by flicking the tongue rapidly.

Sensory specialization

• Example:
  - Some species of birds and bees are sensitive to changes in magnetic fields. Magnetic sensitivity is thought to involve organs containing small amounts of magnetic material affected by the earth’s magnetic field.
  - Magnetic sensitivity is believed to help birds orient themselves during migration.
Sensory specialization

• Example:
  – Weakly electric fish have electric organs that emit a current field that spreads in concentric waves around their bodies.

Sensory specialization

– Weakly electric fish also have electrical sensory receptors (electroreceptors) that register the strength of the electrical field. Perturbations in the electrical field are used to detect objects and transmit information during social communication.

Sensory systems

• Conclusion:
  – Many animals that emit complex forms of energy (color patterns, sound sequences) also have specialized receptors to detect them. Some of these specialized sensory systems also function prominently in their communication systems.

Honeybee

Kingdom: Animalia
Phylum: Arthropoda
Class: Insecta
Order: Hymenoptera
Family: Apidae
Genus: Apis
Species: mellifera

Honeybees

• Diploid animals (e.g. humans)
  – 2 sets of chromosomes, one from each parent; siblings share 50% of their genes
• Haplodiploid animals (e.g. honeybees)

Honeybees

• Haplodiploid animals (e.g. honeybees)
  – Males (drones) develop from unfertilized eggs and have only one set of chromosomes (haploid)
  – Female (queen) has two sets (diploid). One set is passed on to her offspring. So queen and worker bees/drones share 50% of their genes.
Honeybees

• Haplodiploid animals (e.g. honeybees)
  – But all the workers (sisters) in the hive receive the same set of genes from the male (50% shared) plus one of two sets from the female (50% of 50% = 25%) for a total of 75% shared genes.
  – Implications for social behavior?

Specialization

• Specializations of the sender
  – Modifications of body structures for purposes of transmitting signals

• Adaptation to the channel
  – Modifications that facilitate the transmission of signals through a communication channel

• Specializations of the receiver
  – Modifications of sensory and neural systems that facilitate signal reception

Acoustic Communication

Mechanisms of sound production
1. Respiratory structures
2. Beating a substrate
3. Rubbing of appendages

Studying acoustic communication
1. Behavioral observations
2. Acoustic analysis of natural recordings
3. Playback experiments with recorded signals
4. Playback with modified signals

Properties of sound

• Transverse waves – particle displacement is perpendicular to direction of wave propagation
  
  Example: guitar string

• Longitudinal waves – particle displacement is parallel to direction of wave propagation
  
  Most sounds in air

http://www.gmi.edu/~drussell/Demos/waves/wavemotion.html

Properties of sound

• Water waves combine longitudinal and transverse motions. The particles travel in clockwise circles.

http://www.gmi.edu/~drussell/Demos/waves/wavemotion.html
Properties of sound

- Sound has three basic dimensions:
  - Frequency (pitch)
  - Intensity (loudness)
  - Time (length)

Properties of sound

- The frequency of a sound wave, measured in cycles per second or Hertz (abbreviated Hz) indicates the number of cycles each wave makes in one second. The more cycles per second, the higher the pitch we hear.

Properties of sound

- The intensity of a sound wave is measured in decibels (abbreviated dB). The higher the intensity of a sound, the louder it sounds.

Decibel scale

- Rustling leaves: 10 dB
- Purring cat: 30 dB
- Bird singing nearby: 50 dB
- Conversational speech: 60 dB
- Barking dog nearby: 70 dB
- Roaring lion: 90 dB
- Thunder: 110 dB
- Jet taking off nearby: 120 dB

Stages of sound production

1. production of vibrations
2. modification of these vibrations to match biological functions
3. coupling of modified vibrations to the medium in which they propagate.

Body size and frequency range

Sound dispersion

- Sound spreads hemispherically.
- Sound intensity ($I$) decays in proportion to distance ($d$) squared (inverse square law):

  $$I = \frac{1}{d^2}$$

Sound attenuation and frequency

- Atmospheric absorption is an important factor in sound decay (attenuation).
- High frequencies are attenuated more than low frequencies in air.
- Atmosphere acts as a low-pass filter:

Obstacles and sound transmission

- Vegetation (tree trunks, leaves) and other obstacles can obstruct sound transmission.
- **Echoes** are produced when sounds are reflected from an obstacle and follow an indirect path to the ear of the receiver.

Sound power and body size

- Total sound power depends on the size of the animal (animals with small body mass tend to produce sounds with low acoustic power).
- Some exceptions to this rule: cicadas

Obstacles and sound transmission

- Low frequency sounds have longer wavelengths than high frequency sounds and can bend around obstacles.

Source: [http://myweb.dal.ca/mkiefte/](http://myweb.dal.ca/mkiefte/)

Modes of sound production

- **Monopole** - sound alternately contracts and expands in concentric circles around source.
  - alternating compression and rarefaction used by some fish (pulsating air sac)
- **Dipole** - sound source that vibrates back and forth
  - E.g. **stridulation** in crickets
  - Efficiency of sound transmission?
Cicadas (Order Homoptera)

- Medium to large insects with two pairs of membranous wings, prominent compound eyes, and three simple eyes (ocelli).
- Many produce loud sounds by vibrating membranes (tymbals) near base of abdomen
- Rhythmical ticks, buzzes, whines, or musical sounds
- Congregational and courtship “songs”

**Periodical Cicada**

- **Kingdom:** Animalia
- **Phylum:** Arthropoda
- **Subphylum:** Uniramia
- **Class:** Insecta
- **Order:** Homoptera
- **Family:** Cicadidae
- **Genus:** Magicicada
- **Species:** septendecim

http://animaldiversity.ummz.umich.edu/

**Cicada sound production**

**Tymbal**

- Most complex insect sound-producing mechanism known
- Circular membrane surrounded by heavy rings on cicada’s abdomen
- Contraction of tymbal muscle causes tymbal to spring back, producing loud click or pulse (120-480 per second); amplified by resonating cavity in the abdomen
Cicada sound production

Tymbal
• Loudest known insect sound: up to 100 decibels at close range
• Most likely females detect and prefer males with the loudest “songs”

Cicada sound production

• Phonotaxis – orientation toward sound
• Song choruses
• Synchrony or alternation
• “Domino effect” (first song triggers others)
• “Last word effect” (competition for last song)