# BIOL3046 ANIMAL BEHAVIOUR

## LEC 1-INTRO

- Basics of behaviour.

  - **Behaviour** (definition): the aggregate of responses/reactions/movements made by an organism in any situation.

**Tinbergen's 4 Qs**: used to address animal behaviour (FECD; POMA)

- CAUSE Q (mechanism): which stimuli elicits behaviour pattern? What neurobiological, psychological, physiological mechanisms contribute to regulate this behaviour?
- DEVELOPMENT Q (ontogeny): how did behaviour arise during lifetime of individual? How does environment influence development of this behaviour?
- FUNCTION Q (adaptation): why does behaving in a particular way help the individual to survive and reproduce?
- EVOLUTION Q (phylogeny): how did behaviour evolve over evolutionary history of taxon?

**Behavioural repertoire**

- **Innate behaviour**: instinctive and genetically pre-determined.
  - E.g. reflexes, honeybee dance.
  - Triggered by stimuli that must occur within context of the animal's environment.
  - Not all members of species display exact same innate behaviour-modal rather than FAP allows for *variance*.
- **Learned behaviour**: gathered experience and developed overtime.
  - Ability to learn closely related to complexity of animal's nervous system-this allows for FLEXIBLE behavioural patterns.
  - Habituation: decrease in response after repeated stimulus (sensitisation is the opposite-increase in response after repeated stimulus).
  - Imprinting: learning only occurs in critical period. Process is genetically determined, particular object to be imprinted on is learned.
    - Filial imprinting: parental figure.
    - Sexual imprinting.
  - Classical conditioning: learn ASSOCIATION between 2 stimuli. E.g. Pavlov's dogs-bell and food.
  - Operant conditioning: rewarded/punished to learn behaviour.

    - Observational learning: imitation.
    - Insight learning: problem solving; cognitive/mental processes to associate experiences and solve problems.
- Learning can act to modify species-specific fixed action patterns (FAP) i.e. innate and learned behaviours work together-most innate behaviours improve with practice as animals learn to carry them out efficiently.
- Behaviours often have a trigger e.g. FAPs occur in response to a **sign stimulus** or releaser.
    - Sign stimulus (critical portion of an overall stimulus) → releasing mechanism (neural pathway) → FAP (behavioural response).
    - E.g. sexual attraction in sticklebacks.
        - Used different male shape and colour configurations to determine what females were responding to.
        - Females respond to red underside ONLY. Therefore, males red belly is the sign stimulus.
    - E.g. egg-retrieving behaviour in geese.
        - Sight of displaced egg (sign stimulus) → triggers retrieval behaviour in many bird species (FAP).
        - Behaviour can be triggered by variety of objects.
    - E.g. geese prone to **supernormal** stimuli.
    - Stereotypical sequence of events demonstrates weakness of FAPs.
- Behaviour influenced by both genes and environment.
    - Environment can affect gene expression and in turn affects development of behaviour- BEHAVIOURAL EPIGENETICS.

## LEC 2- GAME THEORY & EVOLUTION OF COOPERATION

- Understand the Prisoner's Dilemma Game.

- Game theory is a strategic study, it attempts to understand the best strategies for interactions with other parties.

**Prisoner's dilemma (PD)**

- 2 felons rob a bank and are placed in separate cells.
    - Both stay silent → both get minor charge = reward for **cooperation**.
    - Both confess → both get convicted = punishment for **defection**.

- One confesses, one stays silent → silent goes to jail = Sucker's **payoff**, blabber gets a lesser charge = **temptation to defect**.

- **Payoff matrix**

| | | Blue | |
|---|---|---|---|
| | | Cooperate | Defect |
| Red | Co-operate | R=3,R=3<br>Payoff for mutual cooperation | S=0, T=5<br>Sucker's payoff and the temptation to defect |
| | Defect | T=5, S=0<br>Temptation to defect and sucker's payoff | P=1, P=1<br>Punishment for mutual defection |

- With single encounters, always defect unless both parties' defect as this leads to punishment.

- With multiple encounters, it is better to cooperate.
    - Players **consider future**: If subjects know they will have to meet the player again, they may prefer rewards over punishment. If they will never meet the player again, they should prefer to defect.

- Appreciate common strategies for playing PD.

  **Tit-for-Tat** strategy:

  - Cooperate on 1st move → does what partner does.
  - Defect on 1st move → other players defect back.
  - Avoids sucker's payoff but rewards cooperation.

- Apply concept of PD to common human situations.

  - PD situations in human affairs: economic (petrol prices), political (voting), military.

- Understand place of game theory in evolution of cooperation.

  **Reciprocity theory**

  - If individuals have to repeatedly interact with each other → fitness can be increased by cooperation (opportunities for reciprocity; Tit-for-Tat). Hence avoiding the punishment (P) for mutual defection.

  **Evolution of cooperation among non-relatives (single encounters)**

  - One-time interaction → best strategy is to NOT cooperate on any encounter.

    - E.g. competition for food, steal all of it.

**Requirements for the evolution of cooperation**

- Ability of animals to recognise each other.
- Repeated encounters as in mutualisms.

**Evidence for evolved tendency for cooperation in humans**

- E.g. Western Front War: soldiers fire weapons, but not directly into opponents trenches UNLESS they fire first and cause harm (defect → defect).

- Understand Hawk/Dove and Ultimatum games and how they inform evolutionary theory.

**The Ultimatum Game**

- One player (**proposer**) in a pair of subjects is rewarded a sum of money. The proposer is given the option to split it with the other player (**responder**). Once the proposer communicates their decision, the responder may either accept or reject the offer. If responder ACCEPTS → money is SPLIT. If responder REJECTS → both players receive NOTHING.
- Acceptance rates decrease with lower offers (e.g. $9 proposer: $1 responder) because it seems unfair.
- Results not just subjected to humans; this is also seen in monkeys that are spiteful too.
    - High refusal rate when reward is unequal.

**Hawk/Dove (HD)—aggression and submission**

- When resources are limited (e.g. food, shelter, mates), conflicts/contests may arise.
- Aggressive acts are maladaptive (inappropriate).
- Many encounters only end in display WITHOUT PHYSICAL INTERACTION.
- When 2 individuals meet, the outcome depends on the genetic tendency to be submissive or aggressive.
    - Payoff for attacker depends on strategy (flight/fight) the opponent adopts.

- Calculate the ESS from a HD game.

**Evolutionary Stable Strategies (ESS)**

- Strategy that cannot be invaded/bettered by new/mutant strategy.
- Strategy = genetically determined decision rule = the winning strategy.

- Payoff matrix for an aggressive interaction over a resource (HD game):

| **ATTACKER** | **OPPONENT** | |
|---|---|---|
| | *AGGRESSIVE* | *SUBMISSIVE* |
| *AGGRESSIVE* | Fight (injury) | Aggressor wins |
| *SUBMISSIVE* | Run away (flight) | Display |

- Submissive (S) individuals do well in populations with many aggressive (A) individuals → aggressors fight and injure each other → reduces aggressor population → more resources for submissive.
- Aggressive individuals do well in populations with many submissive individuals → less injury, more winning.
- **Mixture of A and S is likely to be stable**.
- Working out ESS:
    - If 2 individuals meet at some resource worth 40 units and
    - Cost of injury (CI) = -60 units.
    - Cost for displaying (CD) = 10 units.
    - Where ***a* = proportion of aggressors**; ***s* = proportion of submissive** (s = 1 – a).

| **ATTACKER** | **OPPONENT** | |
|---|---|---|
| | *AGGRESSIVE* | *SUBMISSIVE* |
| *AGGRESSIVE* | (40-60)/2 = -10 | 40 |
| *SUBMISSIVE* | 0 | (40-10-10)/2 = 10 |

**AVERAGE PAYOFF FOR AGGRESSORS** = -10a + 40s = -10a + 40 (1-a)

**AVERAGE PAYOFF FOR SUBMISSIVE** = 0 + 10s = 10 (1-a)

**AT EQUILIBRIUM PAYOFFS NEED TO BE THE SAME THEREFORE:**

$$-10a + 40(1-a) = 10(1-a)$$

$$-10a + 40 - 40a = 10 - 10a$$

$$-40a = -30$$

$$a = 0.75$$

$$s = 1 - a = 1 - 0.75 = 0.25$$

## LEC 3-NATURAL SELECTION, ANIMAL BEHAVIOUR & EVOLUTION OF HONEST SIGNALS

- Understand differences between proximate and ultimate causes of behaviour.
  - **Proximate questions**: immediate reasoning behind behaviour.
    - Ontogeny: *development* of animal behaviour.
    - Mechanism: what is *causing* the behaviour.
  - **Ultimate questions**: deeper reason for behaviour.
    - Phylogeny: *evolution* of behaviour.
    - Adaptation: *function* of behaviour.
- Understand that behaviour is subject to natural selection.
  - Signal: e.g. bees shaking to warn predator that it has been seen. They don't just perform this warning signal to any insect, only shown specifically to a certain species of wasp.
  - Shaking is an evolved behaviour—shaking more vigorous when predator is closer to hive entrance.
  - Another related species (*A. mellifera*) to this shaking bee (*A. cerena*) evolved in the absence of the predator wasp/hornet and NEVER shakes/signals. Therefore, more kills are made in *A. mellifera.*
  - *A. cerena* raised in lab also showed same shaking response when wasp was present, hence it can be concluded that this is a genetically based behaviour (innate, adaptive).
- Understand why animal signals must be honest.
  - Shaking sign from *A. cerena* is HONEST. Wasp responds accordingly to **predator prey signal** because it KNOWS it can be killed if it contacts the nest entrance.
    - Bees can kill wasp by crawling on top of it and overheating it through the friction of shaking.
  - **Animal signalling can only be STABLE if signals are honest**.
    - **Predator prey signal benefits both parties.**
    - E.g. saves energy for the bees <–> keeps the wasp safe.
    - E.g. stotting (leaping in the air) in springbok (antelope). Theoretically speaking, this should attract predators. Why do they do this?
      - As an **alarm signal:** warning to OTHERS IN HERD that predator is present.
      - **Social cohesion:** if springbok flee as a group it makes it harder for predator to single one out.
      - **Confusion:** stotting may confuse and distract.

- **"I see you" signal:** springbok signals to predator that it has been seen and can be outrun (individual self-defence).

  - E.g. some signals are deceptive like the eye spots on moths—mimicry. Others can also mimic a toxic species.

## LEC 4-BEHAVIOURAL GENETICS

- Give examples of animal or human behaviour with a strong quantitative genetic component and another influenced by simple Mendelian inheritance.

  - Animal behaviour: muscular contractions in orderly sequences.
    - E.g. Imprint: fist moving figure must be a mother (filial imprint).
    - E.g. Long-necked goose FAP: has to complete action of scooping egg back into nest with it rolls away.
    - E.g. Digger wasp FAP: has to get new prey every time they dig a new hole.

  **Behavioural genetics**

  - The study of behaviour that is **genetically variable.** The **evolution** of this behaviour, the **proportion** of behaviour that is genetically determined (e.g. aggression), and the **identification** of genes influencing this behaviour at a molecular level.

  **Behaviour controlled by Mendelian gene**

  - E.g. pair bonding in voles: comparing 2 different species-Prairie vole vs Montane vole.

| Prairie vole | Montane vole |
|---|---|
| - Monogamous (one partner for life).<br>- High levels of social interest.<br>- Males contribute to care of young.<br>- STRONG expression of **vasopressin V1a** receptor in brains. | - Polygamous.<br>- Solitary.<br>- Males do NOT contribute to offspring care (females raise young alone).<br>- WEAK expression of vasopressin V1a receptor in brains. |

  - V1a is expressed in the **dopamine reward pathway**, which makes prairie voles feel good when cuddling mate.
  - There is an increased expression of V1aR in prairie vole brains that may be responsible for monogamous behaviour.
    - Studies have found that an antagonist to V1aR reduces pair bonding.

    - Transfer of gene into mice make the mice behave more like prairie voles-they become more monogamous.

    - Vector-transferred upregulation of V1aR causes montane voles to seek their partners and cuddle i.e. increase in affiliative behaviour.

    - Promotor region of Va1R contains a microsatellite that is long in prairie voles and short in montane voles. These microsatellite lengths are related to cuddling behaviours in males. Although variation in lengths of microsatellites is NOT the generalised cause of monogamy (not a universal phenomenon).

**Evolution of behavioural genetics**

- Monogamy seems too complex to be controlled by a single gene as a whole behavioural syndrome.
- Easier to imagine a suite of behaviours present in all voles, but the **threshold** required to elicit a response is **genetically variable.**

**Genetic control of queen number in fire ants**

| Monogyne form | Polygyne form |
|---|---|
| - Only one queen.<br>- Heavy.<br>- Fat reserves.<br>- Form new nests on their own. | - Many queens/nests.<br>- Skinny.<br>- Form new nests by colony budding. |

- PGM-3 and GP-9 are allozymes (different structure, same function, coded by different alleles at same loci) that are associated with polygyne queen phenotype.
- BB: monogyne phenotype. Bb: polygyne phenotype (has to be heterozygous or else BB will be killed).
  - Bb ants recognise BB queens with GPB-9 (General Protein Band—an odorant-binding protein) and kill them.
  - GBP-9 is a marker of a whole chromosome (social chromosome) which contains many genes related to social behaviour (SB and Sb).
    - Recombination between SB and Sb is prevented by an inversion.

**Quantitative inheritance of behavioural traits**

- Many traits are <u>genetically influenced</u> but NOT genetically determined. E.g. traits like alcoholism, tameness and IQ are controlled by many genes, but also strongly affected by the environment.
- Requires the technique of quantitative genetic to analyse them.
  - E.g. selection for tameness in the red fox and also in dogs. Characteristics such as number of bites, barks, growling etc. selected to determine tameness.

- Heritability of human behaviours:
  - **Heritability** = proportion of behaviour which is due to genes/phenotype variance.
    - $\mathbf{h^2 = 2 (r_m - r_d)}$
  - Measured via twin studies.
    - Monozygotic relatedness ($r_m$) = 1; dizygotic relatedness ($r_d$) = 0.5
  - E.g. genetics of alcoholism: 18% if adoptees from alcoholic parents (biological) develop alcoholism (different environment).
    - Heritability of alcoholism as a genetic component is moderate, associations are weak.
    - Alcohol and aldehyde dehydrogenases (ALDH): approximately 50% if east Asians inherit inactivity of mitochondrial form of ALDH → leads to build up of acetaldehyde.

## LEC 5-KIN SELECTION & THE EVOLUTION OF SOCIAL BEHAVIOUR

- Define group selection, kin selection and inclusive fitness.

**Types of social interactions** (CASS)

- Cooperation: actor and recipient both benefit e.g. in social honey bees, lions (cooperative hunting).
- Selfishness: actor benefits, receiver is harmed e.g. gorillas.
- Altruism: receiver benefits, actor suffers cost e.g. social insects, Belding's ground squirrel (one "guard" stays in the open to give warning when predator is near).
  - Difficult to explain in terms of Darwinian fitness—different interpretation in everyday vs evolutionary sense.
- Spite: actor and receiver pay cost, but relatives benefit e.g. humans, worker ants eat each other's eggs.

**Hypotheses for altruism—group selection**

- Wynne-Edwards: altruistic behaviour evolves for the "good of species". E.g. populations that are altruistic regulate their size and this regulation prevents extinction of the group.
  - If there are competing groups, those that can regulate population size will outcompete unregulated populations.
  - Therefore, **group selection is NOT an ESS.**
  - Problem with group selection: for a whole group to obtain a single trait, the trait must spread through the population via evolution first. However, when there are many different competing groups, each with their different ESS, selection will result between the different strategies as some are worse than others.