Levels of analysis

- Why do male caribou grow Antlers?
  - **Proximate** (immediate mechanisms – e.g., hormones controlling behaviour)
  - **Ultimate** (why male caribou fight)
    - Q: Why?
    - A: Winning: increases fitness (# of babies)
  - Both of these are important to an animal behaviorist

Tinbergen's Four types of Questions

- **Proximate**:
  - Mechanisms
  - Development
    - What happens when one is young effects animal into later in life.
- **Ultimate**:
  - Survival Rates
  - Evolutionary/Phylogenetic

Monarch Butterfly

- Natural History:
  - How does the organism go about its life?
- Females only lay eggs on milkweed leaves
- Starts as monarch caterpillars
- Several weeks of development because their skeleton is on the outside (***exoskeleton***)
- They shed their outer skin
- Form a ***chrysalis*** before becoming butterfly
  - Undergo changes to become butterfly

- Insects are typically short-lived
  - Most NS insects (like most insects in general) only last a few weeks
  - Insects are cold-blooded (unlike mammals)
- **Special things about *monarchs*:**

1. Able to eat milkweed (which is poisonous)
    - Not only is it able to eat milkweed, it relies on it
    - The caterpillars eat it
2. Monarchs are migratory
    - When they come out in August, they go to one particular spot in Mexico

NOTE: there is no overlap of generations with most insects

- Monarchs that are traveling to Mexico are from the eggs of the previous generation

Monarch Butterfly (***Danaus plexippus***) in NS

- Why they're here:
    - There's abundant milkweed
- However:
    - Cold winters (meaning it's cold, no food)
    - **Most insects** enter **winter diapause)**
        - A **reduced metabolic state**
        - Proximate Mechanism: **antifreeze** proteins
            - Monarchs cannot make anti-freeze proteins like many other insects (because of the Monarch's tropical ancestry).
    - Being tropical (from the **Danaus genus – monarch only one that exists this far north**) + food in North Eastern America
        - Creates pressure to migrate
        - The place they go, in Mexico, is cold but **frost free**.
    - They need to live 8-9 months to migrate and reproduce
    - Movement back from Mexico happens in units of several hops.
        - 4-5 generation hops from Mexico back to NS.

Cost vs. Benefits of Eating Milkweed

- **Benefits**:
    - Obtain poisonous substances, reducing predation (from birds)
        - Greater survival; more offspring
- **Costs**:

- Physiological cost of enzymes needed to sequester **Cardiac glycoside**
  - This means less energy for reproduction
    - Fewer offspring (ultimate cost)

Proximate (how) and Ultimate (why) questions

- Both needed to understand animal behaviour
- **Proximate questions**-
  - Have to do with mechanisms
  - How behaviour accomplished (e.g., sensory systems, hormones, physical, etc.)
- **Ultimate Questions**:
  - **Has to do with Evolutionary Significance**:
    - How behaviour benefits individuals' ability to survive and reproduce?
    - Evolution of behaviour:
      - E.g., does behaviour exist in relatives?

Why do birds avoid eating Monarchs

- (i.e., what is it about monarchs that discourages birds?)
  - Proximate:
    - Monarchs exert toxins from milkweed in their bodies, thus birds don't like them
  - Ultimate:
    - Fewer bird babies

Why did monarchs become poisonous?

- Reduce predation: increases survival: increase offspring

For what reasons do Monarch's Migrate?

- Ultimate:
  - access to an abundant food source
  - Escape cold temperature

Proximate Question: what are the sensory cues that lead to the development of the migratory path

- (likely the magnetism of the earth, polarization of light)

Why do monarch migrate instead of overwintering
- Proximate: can't make antifreeze
- Ultimate: increase reproduction

Chapter 2

Evolution:
- Natural Selection
    - Darwin

Four Premises of Darwin's Theory:

1. **Reproduction leads to an increase in the # of individual in a species**
    - 1 monarch can lay >500 eggs
    - in two generation, if all survived, from 2 monarchs they'll descend 250,000 offspring.

2. **Resources are limited**
    - # of individuals in a species tend to remain constant (e.g., monarchs.

3. **Individuals are not all the same**
    - Individuals vary from one another due to hereditary differences (gene differences).

4. **There is Differential Reproduction**
    - in the population with animals with certain traits having more surviving offspring.

Modern Definition of Evolution:

- Changes in gene frequencies

Reproductive success is the most important

Most traits only give a small advantage

- Long time to become "**fixed**" a consistent feature in the population

IF shorter lifespan is adaptive, but increases reproductive success, then it would likely be selected for.

Evolution:

- Has **no goal**
    - Local adaptation: not necessarily smarter, faster; increased complexity

Natural Selection:

- Only the best adapted to the environment survive to reproduce
- Gradually increase in the population

- Animals with traits that are adaptive are selected for
- "Fitness"
    - animals that have the greatest potential to survive and have the largest number of offspring
- The "fit animals" are capable of contributing more to the gene pool of the next generation than average

Example of Natural Selection

- Cricket vs. paracytic fly (fly name: **ormia achracea**)
- Adult male crickets attract females by rubbing wings together (makes singing noise)
- Females phonotactic (sound analysis)
    - Females prefer males that sing with
        - A **loud** song
        - A **long** duration

Problem: males also attract predators

- Females deposit eggs, larvae burrow inside and eat cricket from the inside-out

Papal Case

- Formed after larvae leave cricket
    - That is, after they exit the body of the cricket

Two opposite forces of selection are acting on the male crickets

- Loud constant singing = increase in mating…but also attracts fly

- **Satellite Males**
    - They're less successful over short periods of time
    - But, they're more successful **over long period of time**.

- Males can be **satellites** and **singers**
- Mutation in Hawaii discovered by **Marlene Zuk** for mutated/hermited satellites
    - mutation for flat wings: can't sing

Fitness Consequence of Mutation

- **Benefits**:
    - Singing Crickets:
        - higher reproductive success in the short term
    - Silent/mute Crickets:
        - lower reproductive success in the short term
- **Costs**
    - Singing Crickets:
        - attract flies
    - Silent/mute Crickets:
        - has to find females.

Future of Hawaii with respect to crickets

- Takes the fly ~7 days to kill cricket
- After infection makes singers have much fewer mattings
- Prior to infection, singers try to make many times with females
- As the number of singing males decreases, more female (mate with flat wing/mute males)

One plausible Future of crickets

- Oscillation of # of flies and singing crickets over time

Fitness of a particular trait depends on population

- Fitness of animal depends on fly population

Flies present: ↑ fitness for flat wing males
Flies absent: ↑ fitness for singers

Chapter 3

Traits: phenotype

- Expression of the animal's blueprints
- AKA select manifestation of genotype

Genotype ≠ Phenotype

- Genotype
  - Genes possessed by an individual
  - Produce phenotype (along with environment)
  - Genes are not the sole determinant of behaviour!
- Behaviours that are not inherited cannot be selected for by natural selection

Why Genotype ≠ Phenotype

- Genes do not directly produce behaviour

- Genes modify behaviour because they regulate physiological function (e.g., brain biochemistry)
- Environment also influences behaviour!

  Given that Genes act indirectly provides a space for other facts to influence behaviour (e.g., environment)
    - Environment can alter the message between gene-behaviour
- Learning also influences behaviour
- Learning important to the behaviour or even simple organisms

Grasshopper Experiment

- Grasshopper has a choice between unhealthy and healthy diet
    - The experimenter gave each diet a different smell
        - Grasshopper learned to go towards a balanced diet smell, even when it changed
    - The grasshopper only wanted the smell for healthy food.
    - Random switching, controlling against grasshopper affinity for the smell its self, did not show a connection – i.e., the grasshopper was interested in the food its self and if smell could predict it.

Learning increased growth (what is better)

- Evolution and animal behaviour
    - Evolutionary explanation of behaviour assumes that much of behaviour is heritable (i.e., controlled by genotype)
- Behaviour has complex relationship with genes (traits are typically **Polygenetic**

Evolutionary theory only applies to behaviour with a large genetic component

- Evolution can only act on heritable components

Evolutionary Psychology

- Some human behaviour is genetically determines

- Some recent research posits that Anger evolved to allow stronger people to resolve conflicts in their favor

Mate Choice in Humans

- Research:
    - **Dr. Bass** studied the importance of money in mate choice
        - He surveyed men and women in 37 countries
        - In 36/37 of the surveyed countries, money was more important to woman than to men (except in Spain)
    - **Dr. Bass concluded that women are concerned about finding a mate with resources**.
        - **Other researchers** noticed that gender wage disparity was a predictor of women's interested in a wealthy spouse

There is strong evidence genes play a role in controlling some behaviour

Artificial Selection:

- Rats ability to learning maze

- (Good maze learner) x (good maze learners) = offspring, over time, that are **good** at learning the maze .
- (Bad maze learners) x (bad maze learner) = offspring, over time, that are **bad** at learning the maze

Mutations can alter behaviour by changing:

- neural functioning (e.g., receptor ion channel)
- Hormonal function (chemicals that are released)
- Other (flat wings).

Drosophila Larvae

- Rovers (move more) vs. sitters
  - Single gene difference

- Foraging behaviour can be altered by food deprivation (i.e., rover vs. sitter)
  - Amount of food in an environment determines phenotype – even with rover gene
- Rover/sitter gene also influenced by other genes (ie., genetic background important (**epistasis**: the effect of one gene depends on the presence of one or more 'modifier genes')
- Rover/sitter (forage) gene encodes an essential gene important for intracellular signaling (PKG)
- Rovers have high PKG activity
- **Takeaway**:
  - **Few genes are dedicated to a behavioural function**.

Genes and Behaviour

- The term "behavioural gene" should not imply that a gene controls or determines behaviour
- Genes influence neural function
- Genes also influence development

- Complex genetics of behaviour means that ***evolution cannot always optimize behaviour***.
- Some behaviours easier for natural selection to modify than other behaviours

Behaviour is not always adaptive

- **Pleiotropy**:
  - One gene has multiple effects
  - Can limit evolution for a particular effect
    - For example, if it has both positive *and* negative effects
    - E.g. Hairiness and nail hardness being on the same gene → have to compromise both, or chose one
- **Gene Linkage**

    - Neighborhood Genes
        - Physically close on chromosome and are often inherited together
        - Hard to separate one from the other – say if Natural selection "wants" one, but not the other (gets easier the further apart the genes are)
- **Epistasis**
    - Gene interaction
        - A gene expression depends on other genetic present
        - You'd have to select for a gene complex to get a desired trait
        - e.g., if you wanted more aggression, you'd have to select for several genes
- **Environment Effects**
    - Environment influences gene expression
        - Example:
            - PKU: can't process a particular amino acid
            - Effects of the disorder depend on diet
- **Species Lack Genes for More Adaptive Behaviour**
    - Evolution can only work on existing genes and fortuitous mutations
        - Example: monarch butterfly not having genes for winter diapause in cold climates
- **Genetic Drift**
    - Loss of variability due to drastic increase in population
    - Typically caused by the animal going through a population bottleneck – i.e., lots of genetic variability has been lost
        - E.g., Cheetahs
            - Low genetic diversity
            - High mortality
            - Poor sperm quality
- **Genetic Drift** (aka **Founder's Effect**)
    - Some island populations founded by a pregnant female or just a few animals
    - Little genetic diversity
        - Thus little variation for natural selection to work on/with

- **Gene Flow**
    - Migration of animals from one area to a neighborhood areas ***dilute*** adaptive genes
        - Animals adapted to a given ecological niche are liable to be diluted by animals adapted to a different ecological niche, reducing fitness for the offspring of such encounters.
        - E.g., anti-predator behaviour in guppies

Anti-Predator Behaviour in Guppies

- Guppies in river of Trinidad
- Upstream of waterfall, there are few guppy predators
- Downstream, there are many guppy predators
- Some guppy species, but morphological behavioural difference

High Predation Guppies (**Downstream**)

- Mature faster than guppies from low predation sites
- Smaller
- Produce ***more*** offspring than low predator (upstream) guppies
- These high predation guppies **shoal** more (which is similar to schooling, i.e., guppies grouping together)

Low Predation Guppies (**Upstream**)

- Take longer to mature
- Larger than guppies from high predation sites
- Fewer but lager offspring
- Tend to solitary (i.e., don't shoal)

Natural Selection Differs for two Guppy Populations

- **High Predation**
    - Being large provides no advantage against predation for the guppies in the high predation environment
    - Better strategy:
        - Mature early, reproduce young

- Anti-predator Behaviour: shoals
- **Low Predation**
    - Less predation if the guppies are large (too large to fit in their only predator’s mouth
    - Shoals increase competition for food with their fellow guppies, thus it’s not something guppies would do if they don’t have to.

- **Test of Hypothesis**:
    - Movement of guppies from one area to another
    - More on this next day

Guppies:

- Differences between high and low predation sites
- Moved from high → to low predation sites

Result of movement:

- Guppies from high predation site ***lost*** shoaling pressure
    - Selection pressure against shoal shoaling
- High to low predation site guppies didn't do well

Guppies moved from low to high predation site didn't do well

- Not liking to shoal hurt them

Genetic diversity actually reduces fitness here

- Specifically, it's gene flow occurring here

Unit of Selection

- Q: Does natural selection work on level of individual ***or*** species?
    - A: Individual!
        - Selection works on expressed phenotype

Group Selection

- Aka "For the good of the species"
- Problem with group selection:
    - Cheaters are rewarded! Aka, cheaters would be selected for
- Rare examples where it does occur, but not usually
- **By and large**, animals **do not** evolve behaviours for the good of the species (for the purposes of this class)

"**Altruistic Animal Behaviours**"

- E.g., Alarm Calls by **Richardson's Ground Squirrels**
    - Alarm Call(er) increases their own risk of being killed by a predator
    - Group Selection

Animals share gene's with close relatives.

- Inf increase number of relatives, another route to reproductive success (i.e., **inclusive fitness**).
- Discovered/first described by **Dr. Hamilton**
- Alarm Cells given to close relatives

Limited Dispersal May Generate Neighbor Related

- Richardson's Ground Squirrels live in clusters
- Aka, animals must live close to their relatives
- Live discrimination

- Increased reproductive success of individual by ↑ gene frequency

Fitness

- Animal's **Potential** reproductive abilities
  - Reproductive success ACTUAL number of offspring
- *Probability* that animal will have surviving offspring (i.e., good health)
- High fitness usually leads to high reproductive success

Inclusive Fitness

- Inclusive fitness includes reproductive success of near relatives
- Estimates relative proportion of <u>shared genes</u>.

We can calculate inclusive fitness scores that reflect the # of genes an individual is able to pass along to the next generation

- Assuming unrelated parents, offspring share about 1/3 genes with parents

  - full siblings share about 1/2 genes with each other

  - First cousins share ~1/8

A = (1/2 + 1/2) ← [children]
  +1/4 + 1/4 + 1/4 + 1/4 ← [nieces & nephews] =

- **2**

B = (1/2) ← [children]
+ 1/4 + 1/4 + 1/4 + 1/4 + 1/4 =

- **1 and 3/4**

C = (1/2 + 1/2 + 1/2)
+ 1/4 + 1/4 + 1/4 =

- **2 and 1/4**

Naked Mole Rats

- Live in harsh environment (the desert)
- Live in underground burrows

- They're small hairless rodents
- Can live in very low oxygen environments
- Love in underground burrows
- Tunnel to tubers (aka roots, which they eat)

- Naked Mole rats are Eusocial
    - Usually found in social insects
    - Communal care of the young
    - Reproductive division of labor
    - A single queen
        - Only the queen reproduces (with just a few males)
        - Workers are stressed into to reproductive diapause (aka they don't reproduce)
    - Other females (and males) work for good of colony (cl
    - Over lapping generations
    - How would Eusociality evolve?
        - How does it benefit the non-reproductive one?

- Hypothesis **Kern Reeves (**at Cornell University)
    - The non- reproductive mole rats help queen
    - Test:
        - **DNA fingerprint**
            - By looking for similarities among variable gene sequences, allowing one to know how closely related given animals are
        - Animals in a **mole rat colony are highly related** – Kern Reeves hypothesis was confirmed.
        - Workers and queen share ~80% of DNA
            - That is, they’re more related to their siblings than they would be to their own offspring
            - Therefore, it’s better to raise siblings (than even its own potential children).

Inclusive Fitness Score for Mole Rat

- Mole Rat (A) is related to each sibling by 0.8
- If (A) mates with an unrelated mole rat, only 50% of its genes would be shared with its offspring
- Inclusive fitness is higher if you live in a colony
- Thus, for the mole rat at least, fitness is higher if you live in colony

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Why not to Start a New Nest, if you're a Naked Mole Rat:

Nest are difficult to build

- Nest are a valuable resource

Better Fitness to Help Rear Mother's Offspring vs. Making a New Nest

- Mole rats are very closely related. Nieces and nephews are more closely related than an individual mole rat's offspring would be
- High risk of dying, trying to build a new nest.

Phylogeny (historical descent of a species) **& Study of Animal Behaviour**

- Evolutionary history through common descent
- Related animals often share similar behaviour

Adaptive Radiation

- Typically occurs when a new species is transplanted on to an island, especially one that doesn't have a lot of animals there already.
- Ancestral species give rise to many new species
- New species occupy new ecological niches
- Darwin saw **Finches**, which had become specialized for various niches
    - Behaviour still clearly related, despite the many niche-specializations – known as Homology.

Homology:

- having the same relation, relative position, or structure, in particular.
- Applies not to just homologous Morphological (e.g., bone, for example) structures, but also behavioural features
- All vertebrates came from a tetrapod, and despite the various lifestyles that have evolved for the various vertebrates, the bone structures, among others, are fundamentally the same.

Analogous Traits (aka Homoplasy)

- Traits that evolved independently but have the same function
- Convergent evolution
- E.g. tool use between corvids (birds) and chimps (primates)
    - Similar, but different historical legacies.

Convergent Evolution

- Squid (cephalopods) eye and the vertebrate eye
- Both squid and vertebrates have excellent vision
- Separated over 500 million years ago

Phylogeny (historical descent of a species) **& Study of Animal Behaviour**

- Related animals often share similar behaviours
    - Homologous behaviour
    - Look at other animals' behaviour to understand a given animals behaviour
    - Moreover, that traits get carried forward (like backwards photoreceptors, in primates) are **not always adaptive**.

To Determine Evolutionary Significance of a Trait

- Determine if trait (e.g., behaviour) is *heritable*
    - If it is not, it cannot be selected for
- Determine **Costs**
    - E.g., time, predator risk
- Determine **Benefits**
    - Enhanced reproduction (direct or indirect)

END OF MT 1 MATERIAL

Mormon Crickets

- Form aggregations (or bands)
- Travel together
- Feed on succulent plants, seeds, carrion, other Mormon crickets

Mormon Cricket Cannibalism

- Cost/benefit of Behaviours
  - Banding in the Mormon crickets
    - Why?
- **Band when there is a drought**

Researchers tracked crickets

- Costs:
  - Increased competition for food
  - Cannibalism is common

Benefits

- Reduced predation
- Increased feeding opportunities (i.e., other crickets – need salt)
- Individuals within bands move to reduce risk of cannibalism

Living and moving in a band, benefit outweigh **costs when food is scare and predators plentiful**

- Selection pressure shifts and compels animals to switch to live in a band

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Causes of Evolution

- Natural Selection
- Gene flow
- Genetic drift

- Sexual selection

Sexual Selection

- Selection for traits that increase successful in mating may not increase survival

Evolution of Sex

- Natural selection favored two types of gametes
- Male: small gamete
- Female: large gamete
  - Carry energy for developing embryo

Why Evolution of Sexual Reproduction

- Some females clone themselves (parthenogenesis) reproducing fish, lizards, insects

- **Costs Of sex**
  - Cost of mitosis (offspring share only 1/2 of genes)
  - If asexual pass on 100% of genes
  - Costs of courtship and mating (energetic, risk of predation, disease)

Benefits of Sex

- Offspring more variable (can respond to changing environment)

Red Queen Hypothesis

- If offspring are variable, it's harder for pathogens to infect all offspring
- Name is from Through the Looking Glass – by Lewis Carroll
- Hosts a constant evolutionary arms race with parasites and pathogens

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Sex and single minnow

- Vr Jenhook study in Mexico
  - A species where some are sexual, other's are asexual

- Asexual minnow population – more parasite
- In lab, no parasites, a sexual reproduction more rapidly than sexual minnow
- Genetically diverse sexual minnows outperform asexual in presence of parasite
- Cost of sex less than costs of parasitic infection

Experimental Evidence

- Minnow study
- Asexual populations have difficulty evolving resistance to pathogens (Red Queen Hypothesis)

Genetic diversity

- Sexual form will outcompete asexual in diverse/dynamic environment

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Traits that increase success in mating will be selected for

- Sexual selection differs between the sexes in most species

Bateman's Principles

- Female Eggs expensiveness limits the number that can be male
- Males limited by the number of eggs can be fertilized
- Females showed guarding eggs against fertilization by low quality sperm

Sexual selection

- Sexual selection can lead to sexual dimorphism vs. natural selection which acts on both sexes equally
- Eggs are the limiting resource to both sexes in most cases
- Females often have to choose the best mate, best genetic quality
- Females tend to take fewer risks to mate

Models of Sexual selection

- **Direct benefits**
    - Providing females with a physical resource (shelter, food, paternal care) (Nuptial gifts)
    - Selection favors those with the best gifts
- **Indirect benefits**
    - Genetic quality
    - Increase of offspring quality, increase female fitness
    - How do they know?
        - Elaborate ornaments may increase predation, but showing that if they still survive it displays they are of good quality of genes
        - Prevents cheats, the cost of ornaments is high and may lead to death
        - Natural selection and sexual selection may act in different directions

Handicap hypothesis

- shows that male is strong
    - e.g., peacock

Hamilton-Zuk hypothesis

-eg European blackbird and their bill

- Females prefer disease free males
- Avoid disease (**direct**)
- Genes are disease resistant (**indirect**)

Scorpion flies

- Males bring food items to females

  - -Direct benefit
- Males who give small gifts are rejected or have short copulation time

Peacock

- Males large and colorful
- Females drab
- Larger male tail= more mating
- Tails trimmed decreases mating
- Offspring with fit males live longer than unfit
- Large tail is an honest indicator of male genetic quality

The Caribou

- Females can only have *1 calf per year*
- Males have harams and a such many may not have access to females, a small percentage of males do most of the mating in a herd
- These mating systems lead to the major sexual dimorphism

European blackbird

- Bill is normally orange
- Becomes pale when sick
- Must be based off a limiting resource
- Orange coloration requires carotenoid, they only have a finite source

Carotenoid is important for the immune system function, as such when you are sick you lose bill colour as carotenoid is used

Small males, how do they mate in these communities

- Different species may have different types of males
- **Bluegill sunfish**
- All genetically linked but leads to different behavior
  - Parental- the male looks after the offspring, fans eggs, protects from predators, the female lays eggs and then goes of.
    - The male makes a nest and the female selects based on the nice nest
    - Often large, muscles need to fan eggs and reduce predation
  - Sneaker- will sneak in and fertilize some eggs in another (parental) males nests
    - Smaller, but have very large testes
  - Satellite (female mimic)- males look like females enters the nest during courtship and acts like another female, confusing the other male and then releases sperm

Sexual selection

- In most species multiple mechanism occur at once
- E.g. female choice and male competition

Mating systems (4 types)

- Monogamy (1m:1f exclusive)
  - higher survival ship of young,
  - may reduce investment for f
  - not favorable to males
- Polygyny (1m: xf exclusive)
  - Ideal for males
  - F costs are high, full cost of reproduction
- Polyandry (1f: xm exclusive)
  - may increase survival of young but not necessarily #, cost sharing

- males should be pushed as way as best strategy is multiple females
- Polygynandry (xm: xF non exclusive)
  - good for males, have access to multiple females but not exclusive
  - NO costs sharing for F
- Different selection pressures on different species sexes (different investments made)
- Mating systems have different implications for mating success for males and females

Monogamy

- Common in birds, rare in mammals (some examples e.g. Oldfield mouse)
  - Males can frequently take over much of the parental care e.g. feeding, incubating eggs
- Biologically, females in mammals are bound to take most of the costs of reproduction
  - Males often can not aid, due to not being able to lactate
  - X< 10% of mammals, frequently social structures
  - Mate assistant hypothesis
- Selection pressure for monogamy
  - Few female (low pop. Density)
  - Dependent young
  - Resource defense (eg nest)
- Monogamy without parental care
  - Mate guarding hypothesis
    - Male stays around to prevent the female from mating with others
    - Depends on sex ratio lots of males, few females
    - May have little impact on female reproductive success

Oldfield mice

- Why monogamous
  - Must benefit males or would be selected against
  - Mate assistant hypothesis

    - Two parents are required to raise the young, due to environment
    - One must stay to guard pups, the other must forage for both
    - Most common reason to monogamy
    - Assures the male is rearing his offspring and not others, increasing and required for his reproductive success
  - Alone female reared less than 1 pup successfully
  - Females + males reared 4 pups successfully
  - Males need to keep pups warm and clean
  - In the field nests are far apart, wandering males may be preyed upon
  - In field females alone can not rear pups
  - Nests are rare, require large investments
  - Non monogamous choices are best

Mating Systems

- **Old field mouse**
  - Monogamy, necessary
- **Mate Guarding**
  - Example: the clown shrimp

Other selection Pressure for Monogamy

- Female-enforced monogamy

Razorbill (**seabird**)

- Attack make patterns if ‘intruded’ females occur
- Yellow-breasted chat birds
  - Attack females near nest

Monogamy in Birds

- Memory birds biparental
- Males can invest in offspring egg (unlike mammals)
- Most birds are **“socially” monogamous**

Socially monogamous

- vs. sexually monogamous

Extra-pair copulation (**EPC**)

- In most species, males and females have EPCs
- EPCs produce *some* offspring (not huge amounts)

Why EPC’s:

- Males:
  - Increase number of spring
  - Cost of rearing young by other males
- Females:
  - Good genes
  - Maximal genetic diversity of offspring

- Both: fertility insurance (both want fertile mates)

Monogamy

- 1 male, 1 female

Polyandry:

- Female with several males
- Typically males rear the offspring
- Example: Jacana (type of bird)
    - Jacana: predation pressure has resulted in role reversal between males and females
    - Jacana females hold territories
    - Next sites rare and clumped
    - Once eggs laid, male left to guard
    - If male deserts, no reproductive success (predation)

Conditions for evolution & maintenance of **Polyandry with Paternal Care**

- Female reproductive success enhanced
- Males:
    - Young will not survive without paternal care
    - Other option(s) reduce fitness

Polyandry without Paternal Care

- Social inset (e.g., bees)
- Queen mates with many males. Male dies after mating (abdomen rips off to temporally block other males from entering female)
- Male unlikely to mate again, even if it somehow survives

Multiple mating's can be:

- **Costly**
    - Disease
    - Time
    - Predation
- **Benefits**
    - Sperm replenished
    - Material benefits
    - Reduced male harassment (for females – male stops bothering female after)

- Females of most species mate multiply

Greater Disease resistance in offspring if female mates with multiple males

- Likely in males with virtually no hope of other mating
- Extreme example:
    - Sexual cannabism
        - E.g., red black spider (female eats male after mating – male actually offers itself as food).

Polygynandry Mating Systems

- Both males and females mate multiply (e.g., dung fly)
- No paternal care
  - No assurance of paternity

- Mating system can very within one species
  - Dunnocks
  - Species can be monogamous, polygynous, polyandrous, etc (all types)
  - Males and females look alike
    - No sexual dimorphism means natural and sexual selection acting in the same way

- Dunnocks
  - Early in the breeding season, females compete to establish territories
  - Males then establish territories overlapping as many female territories as possible
  - Monogamous vs. polygyny depends on male territory size
  - Larger female territories more likely polyandry
  - Males try to get as many female territories and thus exclusive breeding

Fig 8.13 (honestly, just look at this figure for this bit…)

- Dunnock Study
  - Birds were banded
  - Supplementary feeders
  - Female territories smaller
  - Polyandry decreased, polyandry
- Under Good Conditions:
  - Enough food that females require less male help to rear young
  - Females closer together
  - Favor polygyny

Under Poor Conditions

- Females require male assistance to rear young
- Larger territories needed for foraging female farther part
- This condition favor monogamy

- Female territory size depends on resources female competitive ability
- Male territory size depends on male competitive ability
- Existence of beta males depends, in part, on density of male; male completive ability

In most species, females mate with multiple males

- Polyandry
- Polygynandry
- Some forms of polygyny (e.g., some Lekking species)
- Social monogamy

Integrate proximate and ultimate –case study- Emperor Penguin

- Emperor Penguin (Aptenodytes Forsteri)
- Natural history
  - Flightless bird of the atlantic
  - Related to petrel and albatross (other sea birds)
- Emperor Penguins are highly specialized
  - Adapted for marine environment
  - Wings act like flippers
  - Bones are heavy
- They're excellent swimmers
- Still require land for molting and breeding

Emperor Penguin

- Long life (live 20+ years)
- Sexual maturation takes a long time: 4 to 9th
- Little sexual dimorphism
  - Social: breed in large colonies (20,000 birds)

    - Forage at sea in groups
    - Coordinate hunting

Communication:

- Court calling
- Breeding pairs have distinct calls (individual recognition)
- Calls used to find chick (contact calls)
    - Penguins only feed own chicks

Food:

- Eat fish, cephalopods (e.g., squid), crustaceans (e.g., crill)
- Must compete with fish. Unlike Fish, they must breath air

Life Cycle:

- Jan-March at sea feeding
- Mar/April – Return to land, mute, lay 1 egg
- May/June – Female returns to sea, males incubate egg (~64 days)
- August – Females returns, male goes to sea
- If female late, male regurgitates oily substance to feed chick
- Sept/Oct: parents alternate in bringing food to chick
- When chick 45-5o days old, both parents to sea, bring back food.
    - Chick joins crèche (group of young animals)
- Jan. Chiches, adults return to sea

Natural Selection: **Emperor Penguin**

- Predators:
    - Leopard seals, sharks, skuas (type of bird, can only eat Emperor Penguin chicks, not adults)
    - 2nd year, 95% survive to 3rd year
- Survival
    - Most eggs hatch (77%)
    - About 70% of chicks live to go to sea
    - Chicks grow quickly – if not, too small, to little fat to serve cold
        - Heaviest return to sea at first (~12.6 kg)
        - If Less than 5kg at end of season die

Penguin Reproduction

- Monogamous
- Typically change mating systems
- No nest
    - carry eggs on feet

Cost of Reproduction

- Female:
    - Egg production (egg 2-3% of body weight – 450 g) feeding young
    - Prior to breeding season,
        - 28 to 30 Kg
    - After: 30 to 24 kg
    - Most females (98%) survive breeding season
- Males:
    - Incubate egg feeding of young
        - May/June – remale return to sea – Male incubate egg (~64 days)
    - Prior to breeding season: 35 to 40kg
    - After Breeding season 22-25 kg
    - Note: Males lose a larger proportion of their body weight!
    - Some males die (85% survive breeding season)

- Problem for male penguins
    - When on land, no food
    - Incubate egg during Antarctic winter
    - Cold
    - No liquid

- **Costs**:
    - Cold, no food or shelter
    - Specialized adaptations required to survive
- **Benefits**:
    - No predators in winter
    - No predators in early spring (when chicks are very vulnerable)

    - No land predators of adults

Moa and Dodo birds – also ***were*** flightless (but now are extinct)

- i.e., flightless birds can be very easy prey…

Penguin Behaviour

- Breeding in Antarctic winter is a unique ecological niche
- Only possible because of physiological adaption
- Tolerance for long-term cold

Physiological Adaption

- Cold:
    - Insulating Feathers
    - Blubber
    - Counter-current blood system (arteries warm up veins, so returning blood is warmer than it other would be)
    - Huddle
    - Slightly lower body temp than other birds
    - Lack of food during egg incubation
        - Special metabolism for fasting
            - Increase use of fats (can use fat as energy in brain – most animals can only use glucose) and proteins
            - Decreased metabolic rates when incubating of eggs (they sleep 70% of the time – which is possible because no predators, not feeding)

Limits to Physiological Adaption

- Penguins body temp is about 2 degrees celsius less than other birds
- Why not lower?
    - Many enzymes require high temp for maximal efficacy
    - And, of course, Egg requires warmth

The Antarctic Climate

- Harsh climate, two parents required to raise young
    - Favor monogamy or polyandry

    - Selection pressure on males favors monogamy. Little counter selective force on females for polyandry

Penguin Behaviour

- Penguin evolved to take advantage of predator free space
- Required a number of behavioural changes
    - Huge increase in male investment
- Males now invest *more* than females. (Males choosy and search for the fattest female).
    - Females also choosy

Physiological Adaptions have Costs

- Egg/chicks need care for several months
- High levels of prolactin maintain parental care (that is, this is a hormonal mechanism responsible, at least in part, for parental care)
- Prolactin levels reduced abandons chicks

- If chick dies while parent at sea, some parents try to "kidnap" another chick.
- Parent has fight to defend chick
- Chick sometimes killed during fight

Kidnapping Penguins

- Reduced prolactin levels in penguins with dead chicks
- Penguins did not kidnap chicks
- Kidnapper's fitness not really impacted (little risk of injury)

Human Impact on Penguins

- Over fishing reduced food for penguins
    - Decreased weight aka decreased male survival during egg incubation
    - Decreased chick weight, decreasing chick survival
    - Killed in human fishing nets (aka, as by-catch)

Global Warming

- Increased temp. more competitors, predators
  - Fewer defenseless on land
  - Competitors do not have to pay costs of adaption
  - May increase male in chick survival

Tourism

- Can increase stress in the penguins – unclear if this is deleterious
- In short, don’t go to antarctica. Leave the animals alone. Don’t be that guy.

In closing for Penguins

- Environmental physiology, parental + sexual selection explain behavioural patterns

Chapter 3: Proximate Mechanisms

Two most important physiological systems regulating behaviour

- Nervous System
- Endocrine System (hormones)

Immune System also regulates behaviour

Immune System and Behaviour

- Disease is a major selective force
- Selection will favor animals that can resist disease
- Immune System can alter behaviour to favor recovery from illness

<u>Pathogens</u>

↓

Immune system

↕ Cytokines

Nervous System

↓

Change Behaviour

Sickness Behaviour

- changes in behaviour when ill
- decreased appetite, activity
- Increased sleepiness

Activated by factors secreted by immune system (cytokines)

Receptors in brain for cytokines

- Aids recovery

Illness-induced Anorexia (loss of appetite)

- Increases immune function
- Prevent pathogen access nutrients

Parasitic Manipulation of Behaviour

- Parasites manipulates host

    - Parasites activity changes host behaviour to enhance parasite reproduction (e.g., transmission)

"Natural Zombies"

- *Parasitic* wasp (cotesia congregata)
- caterpillar (*host*) (Manduca sexta)

Cotesia Congregata Life cycle:

1. Stay in host
2. eat blood
3. then drill through body wall of caterpillar
4. spin a cocoon

Host Behaviour Manipulation

- Wasp suppress host feeding and locomotion
- Host becomes zombie

Note: Change in host behaviour not due to debilitation

- Intact righting reflex
- Intact defense

Caterpillar dies within 2 weeks, however

Wasps need living host for successful reproduction

- If the caterpillar host dies, the host gets overcome by faunal invader, rot (decay of host), etc.

Also for protection caterpillar defends parasites

- Host Anorexia Benefits wasp
- Wasp *needs* living host to protect from predators

END OF MT 2 MATERIAL

Host has cytokines manipulates

Parasitic manipulation

- Caterpillar stops eating when ill
- Immune system sends chemical signals (cytokines) to brain which halts feeding
    - Shown it is indeed cytokines in lab by injecting insect cytokines (and it does indeed stop feeding)

Natural Zombie

- Parasitic Wasp: over-activated immune/neural connection
    - Prevents “off-signal”

Male Color

- **Male House Finches**
    - Red factor color due to carotenoid
    - Must be obtained from diet – and carotenoid is rate
        - Only males good at finding such food can get it
    - Differences in male coloration due to difference in diet

- Why do males want to be red?
    - Hamilton-Zuk: Sexual selection
        - Females like males that are more red because it signals male heath
        - Did experiment:
            - Injected house finches with bacteria and found that redder males recovered faster, suggesting it is a honest signal of male health

Why is red color related to disease resistance?

- Carotenoid is important for immune system

    - Female zebra finches prefer bright red and yellow males
    - Red and tallow pigment made from carotenoid
    - Healthy males put more carotenoid into pigments, males fighting infection use carotenoid to suppress infection (TRADE OFF)

Carotenoids → Color
→ Immune System

Blount's Study

- Same males fed Carotenoids
- After 8 Weeks, supplemented males had brighter color
- Females preferred supplemented males
- Supplemented males depends stronger immune response
- Study demonstrated that carotenoid indeed improves immune response
- If weak males invest most of their carotenoid in pigment, they will have reduced immune function (trade off)
- Therefore, a strong honest signal

Animals have finite responses
Trade offs reduce one trait to increase another maximize fitness

Why do house finch females prefer red

- Direct benefit
- Redder males feed chicks more
- Sons better foragers (heritable trait) find more carotenoid, become redder, and male desirable males
    - Sexy Son Hypothesis
- Proximate Mechanism
    - Hormones and Behaviour
        - Chemicals secreted into blood by endocrine gland
        - Allow animals to alter behaviour internals and external conditions change
        - Behavioural effect
            - Behaviour triggered by hormones

        - Organizational effect:
            - Hormones with long-lasting behavioural effect
            - Typically a critical period

Hormones and Behaviour

- Hormones can influence behaviour because the cells of the brain (neurons) have receptors for hormones)
- Hormones can alter neural function, resulting in behavioural changes

Hormones and Behaviour in Animal Behaviour

- Comparative approach
    - Examine differences/seminaries across species
    - Exam evolution of hormonal system

Hormones:

- Many hormones have both behavioural physiological effect
    - E.g. testosterone matures sperm in all vertebrates; also cus male sexual behaviour in many vertebrates
    - Same hormone promotes sexual maturation, also sperm maturation

- Evolutionary forces and hormones
    - Connects between hormones and behaviour under both natural and sexual selection
        - Can vary across species and environment

Hormones and behaviour

- To test behavioural affects of hormones
    - Hormonal level should correlate with behaviour
    - Remove Gland, behaviour should disappear
    - Reintroduce hormone (behaviour should re-improve)
        - Used physiological amount (and it does?)

- Testosterone
  - Is different from most other hormones because it is able to enter directly into the cell through the cell membrane
    - All steroid hormones can do this
- Red Deer
  - Seasonal breeders
    - True of all Nova Scotia animals
    - Some times of the year are better for rearing young than others
      - Not a lot of food available in winters
  - During fall breeding season, the testis will secrete testosterone
  - Usually, testis have no function, until fall time; this is when they begin secreting testosterone
    - Induces sperm maturation
    - Also induces male mating behavior
      - Ie. Fighting to get access to females
  - Castrating reed deer in the spring will result in NOT mating behavior in the fall
    - The castrated males will behave as if it's not the fall mating season
- Lab Rat
  - Used as medical models for many diseases
  - Can breed all year round (no specific breeding season)
  - Male rats are territorial and can attack intruder rats
    - When an intruder male is placed in the cage of a resident rat, the resident rat will attack
  - There's a correlation between aggression and levels of testosterone
    - The more testosterone the male rat has, the more aggressive he is more likely to be
  - Castrating the male rats will decrease their tendency to fight
- Humans and Testosterone
  - It is hypothesized that testosterone levels will correlate to aggressive behavior
  - Experiment done to measure aggression
    - Verbal aggression:

        - Experimenter would insult a participant and, if the participant insulted back, it would be recorded as aggressive behavior
            - Didn't really work because females were found to be more aggressive than males
    - Survey:
        - Aggressive behavior did not correlate with levels of testosterone in men
        - Aggression not really (if at all, it'll be subtle) correlated with testosterone levels
    - Castration in Humans
        - Castrated males were castrated due to accidents or cancer
        - Decreased their sexual desire (libido), however there was no change in aggression
- White Crown Sparrows
    - Seasonal breeders
    - Establish territories during breeding season
        - Males come in to defend a territory against other males
        - Females come in to mate with the males with the best territory
    - Bi-parental care
    - A lot of male-male competition
    - Castrating males results in taking their testosterone away
        - Not going to fight for territories anymore
    - Loses territorial behavior
    - They will however continue to mate
    - Testosterone cues territorial behavior, however it doesn't affect mating behavior
    - Increasing testosterone levels in some male birds did not end well
    - Usually after mating, males will focus on feeding the young rather than defending territory
        - Found that the males injected with extra testosterone would focus more on defending territory rather than feeding young
        - Some of the offspring would starve and die

    - It is essential that testosterone levels drop following mating so that the males could help rear the young
- Red-sided Garter Snake
    - Live in Manitoba
    - Hibernates in the winter
    - The very first sign of spring, the males come out first and go hunting for females
    - Follow pheromone trail
        - Females give off scent as soon as they come out of their nest
    - No parental care of young
    - Mating ball behavior
        - A huge number of males will surround a single female and try to mate with her
    - Castration study of male snakes (Castrated in winter)
        - Had normal reproductive behavior in the spring
        - Testosterone cues sperm growth when food resources are high
        - Sperm is stored over winter during hibernation

- Whip-tailed Lizards
  - There is a large group of these species
    - Within them, some of them are sexually reproducing, however there is a closely related species that is asexual
  - Seasonal breeder
    - Hormones cue breeding season
    - Sex hormones turn on sex behavior
    - Don't show sexual signs any other time than breeding season
  - Typically, males have low testosterone levels throughout the year until season of breeding
  - Female receptivity cued by estrogen
    - Cues female sexual behavior
    - Typically, low levels throughout the year until breeding season
  - Induced ovulation in females
    - Female doesn't release egg from ovary to be fertilized until she's had some mating experience
    - Essentially, she doesn't put her egg out until she knows what she's doing in the sack
    - After ovulation, progesterone is released which turns off sexual reproduction and sexual behavior
      - Changes her behavior from looking for mates towards more maternal behavior
        - Ie. Looking for a nest for the eggs, incubating eggs, etc.
  - *C. uniparens* are the asexual species
    - Females can make genetic clones of themselves through their eggs
    - These animals don't receive any genetic information from the males
    - These species are ALL females
      - No males at all
    - Must be mounted by male in order to induce egg release
      - Since there's no males, males from another species have to go through the motions of mating so that the female can develop her eggs

            - Female just digests the sperm
    - Sometimes, females will mimic the behaviors of the males and will mount other females
        - A little girl on girl action, but one female shows male reproduction behavior
    - Increase in progesterone causes male mounting behavior in females
- *C. inornatus* is a sexually reproducing species
    - Consists of both males and females
- Remove ovaries from *C. uniparens*
    - Females would not mount other females
    - Injecting estrogen did not induce mounting behavior
    - Injecting progesterone induced mounting behavior
- Castrate male *C. inortnatus*
    - Injecting testosterone caused all males to mount
    - Injecting estrogen caused no males to mount
    - Injecting progesterone, 1/3 of castrated males will begin to mount females again
        - This is weird because they don't have the glands that secrete progesterone and have never had it in their systems ever before
        - Examining the brain of these lizards
            - Found receptors for both testosterone and progesterone in area that controls male sexual behavior
- *C. uniparens* descended from mutant *C. inornatus*
- Circuitry for both male and female sexual behavior often exist in an individual
    - Will perform typically male or female behaviors with right hormonal environment

♦ Testosterone and Behavior
- Species dependent
- In most species, it cues sexual behavior and is required for it
- Can activate male-male competition, if it is part of that animals typical behavior
- Induces development of sexually selected traits

        - Ie. Peacock tail
- Costs of Testosterone
    - Costs of making it
        - It's a steroid that must be made out of cholesterol
    - Males don't produce high testosterone levels for a variety of reasons
        - Increased risk of injury if not physically large and powerful
            - Small weak males that get into fights will get beat up, thereby reducing fitness
        - Increased risk of predation
        - Reduced feeding
- Testosterone and the Handicap Hypothesis
    - Red wing blackbird male behavior is driven by testosterone
    - Testosterone is also responsible for the red coloration on their wing
        - Advertises to males that they are tough and advertises to females that they are good mates
    - High levels of testosterone are the males with the best territories and have the highest reproductive success while low levels of testosterone is found in the loser males
- Behavior can influence hormones
    - Depending on what happens to an animal in their environment, they have to be able to drop the levels and increase the levels so as to respond to environmental stimuli
    - Ie. Fighting behavior in Lobsters
        - They fight to defend shelters and territory
        - Fights can result in damage
        - Losing lobster should withdraw
        - When a lobster loses, he drops his hormone levels and reduces fighting behaviors
        - Serotonin key hormone for fighting behavior in lobsters
        - Injected some lobsters with serotonin and found that they kept fighting even when they were losing and couldn't stop fighting

Moths are an old insect group

- Bats use ultrasound sonar to hunt at night
- Months shifted to being night active from being diurnal butterflies to avoid predators

Moths and Bats

- When bats close by, moths fly away
- When bats are very close, moths "power dive"

Moth Ear

- One on each side of the abdomen
- **Tympanum** (eardrum) and two receptor cells
- (neurons, A1 and A2)
- Ear tells moth direction and distance to bat
- Evolved from pre-existing mechanoreceptors
- Sound pressure waves stretch tympanum
- Receptor cells depolarize
    - If depolarization occurs, action potential occurs
- Receptor cell synapse onto interneurons → activate → motoneurons.
- Results in a charge in flight direction

How do ear supply direction and distance information to the moth?

- tympanum responds to ultrasound only (well beyond human hearing at ~60,000Hz)
    - A1: sensitive to sounds only of low to moderate intensity
    - A2: fires only in response to low intensity sounds
- As best approaches A1 fires
    - A2 increases firing rate as best approach and bat becomes louder

A1: Sensitive enough to detect bar 30m away (meter or mile???)

A2: Firing rate is proportional to intensity → sufficient intensity triggers **power dive**

A2: Firing causing moth to move away from bat

If bat close, the bat's call is very loud and thus A2 becomes activated

Use it or Lose it

- Evolution does *not* stop once a sensory system is in place
- All sensory systems have costs

Moths with no bats:

- Moths in Tahiti
    - Moths in Greenland and Tahiti thousands of years no bats
    - Moths developed away from bats
    - **Dr. J Fallard** recorded electronic activity in auditory area of moth in response in USA moths
        - Tahiti moths have poor hearing by comparison
    - No selection against mutation that decreases hearing
    - Moths in Tahiti are not completely deaf, thus their hearing is slowly degenerating
    - Low Cost system (??? – messy note)

Female Crickets

- Can hear 3KHz to 100KHz
- Male crickets call 4-5khz
- Fly to males (**phonotaxis**)
- Prefer *loud* males
- Females must also avoid bats (50-80Khz)

How does female know to fly away from bats but fly toward males?

- Heavy selection against "incorrect decision"
- Different receptor cells response to low or high frequencies

Foraging in Honeybees

- When they emerge, they're nurse beers
- Older adult honeybees forage fro pollen and nectar
- Foragers *must* be able to find food source and return to hive
- Requires extensive information processing
- Brain in beers contains mushroom bodies

In Hive		**Out of Hive**
Nurse Bees	→	Foragers

Foraging in Bees

Juvenile Hormone (JH) increases in bees as they become foragers

How do bees become foragers?
- JH higher in foragers
- Removal of the gland that produces JH (corpus allata) delay foraging behaviour
- **Allotectomized** (gland removed) bee given JH
  - (forage at normal time)
- Mushroom bodies are larger in foragers than nurses

Evolutionary Forces on Nervous System
- Evolution acts indirectly of Nervous system via behaviour
  - N allows complex information processing
    - Can compensate fro a lack of claws, etc
    - Allows animal to optimize behaviour depending on conditions

- Most animals have "budget" model of the brain
  - Why?
    - Brains have costs (they're expensive)

Cost of Information processing
- Human brain
  - 2% of body weight
  - but consumes 20% of metabolic output
  - consumes 15% of cardiac output

Is it ever an advantage to be stupid?
- Similar brains:
  - They're cheaper
  - Reliable (i.e., less flexible, less influenced by environment)

Selection for smaller brain
- Animals need neurons to solve problems (e.g., find food, mates)

- What if animal shifts to a new ecological niche? Fewer problems solved

Selection for Smaller brain

- Selecting for smaller brains in Platyhelminthes flatworms
    - Class: Turbellaria
    - Class Cestode (tapeworms)
        - ~ such 5,000 species

Selection for smaller brain

- Turbellaria
    - Complex gut
    - CNS
- Class: Cestoda (tapeworm) – 5000% Species
    - No gut
    - Sense organs much reduced
    - No well formed CNS-Nerve Plexus

Cestodes have fewer "problems" to solve

- If you have fewer neurons more energy for reproduction

Cognitive Ethology

- Learning and "intelligence" from an evolutionary perspective
- Learning is adaptive
- Ability to learn is at least polygenetic

Benefits to Greater Processing Power

- Honeybees
    - Foragers require complex spatial learning
- Social Animals
    - Need to remember relationships and members of the group.

Evolution of information processing ability

- *Older view*:
    - Intelligence is a global property
    - Animals could be ranked for intelligence

    - Large cortex (e.g., frontal lobes) required for abstract reasoning

- *Newer View*:
    - Cognition consists of specialized 'modules' that have been shaped by evolution to solve species-specific information processing problems.
    - Cognition should be viewed as a suite of adaptive traits
    - Selection to minimize costs leads to increase in discrete abilities, not necessarily overall ability
    - Therefore, cannot easily rank animals. Rank may differ depending on task
    - Area devoted to a task may be enlarged, but not whole brain

Small brains can be powerful at specific tasks

- Pigeons can form abstract concepts
- Irene Pepperberg – Worked with Alex the Parrot
    - Alex had the brain the size of a walnut and no frontal lobes
    - Capable of categorizing things

Power of Small Brains

- Honeybees
    - Capable of complex learning (navigation)
    - Beers can navigate using sun as compass (requires map and clock)
        - Also use landmarks
    - Bees use symbolic language
        - Karl Von Frisch (won the Nobel Prize)
        - Waggle Dance gives direction and distance information

- Honey Beer Dance
    - Bees forage for nectar source (e.g., flowers)
    - Bees "tell" other beers where to find the food source using the waggle dance
        - Honeybees foraging up to 8KM from hive
        - Dances highly accurate
- Duration and angle of dance gives position and size of food source

- Signals direct route, even if worker bee flew around obstructions, etc.
    - Therefore, bees can be dynamic (??)

Duration of dance

- Every addition 75 milliseconds of dance means additional 100m away
- Direction (angle) of dance indicates direction of food source from the hive.

Honeybee Dance

Bees forage for nectar source (from flowers, for example)

- Bees tell other bees where to find food via waggle dance
    - Accurate up to 8km
- Duration and angle of dance gives position and size of food source
    - E.g., straight down means go 180 degrees away from the direction of the sun.
    - 40 degrees to the right says fly 40 degrees to the right of the sun
    - Dancer bee takes into account the current position of the sun, compensating against the time it took her to return.
        - (i.e., dancer takes care of where food is given present position of the sun)
            - Signal is the direct route, even if worker beer flew around obstacles
                - There, bee can extrapolate direct angle of return flight
            - Longer the waggle dance, the further away the food is

Test of the Bee Communication

- Michelson made a robot bee
    - Robot bee danced
    - Robot bee could be used to send beers to select spots
    - Proof that the dance signals food location and that the food signal is not being transmitted by some other means (or modality even), such as an olfactory signal.

Delayed Response Task

- Type of learning problem
- Tests whether animals can keep and object “in mind” when it cannot see it
- Bee learned that red square indicated flower with food, and would go to the flower with the red square when it saw it.

- Then researchers put up solid barrier and then took away the red square
    - found the bee couldn't "keep in mind" the location of the food giving flower

How smart are Bees?

- Delayed response test
    - Poor performers
    - But have excellent spatial communicating skills
    - Has needs to survive
    - Modular intelligence
        - Different types of learning ability may not correlate within a species

Evolutionary forces on Learning and the Brain

- Some animals rely on hidden food to survive the winter

Clark's Nut Cracker

- Memorizes location of 30,000 nuts (pine nuts)
- Hypothesis:
    - Rely on hidden food cache will select for increased memory capacity and larger brain areas developed to that task (selective brain areas will be larger)
        - To test:
            - Comparative study of food stopping behaviour and memory
            - Comparative study of food storing behaviour and neuroanatomy

Food Storing in Birds

- Clark's Nutcracker
    - Live and breed at high elevations (the Rockies)
    - Winter: cold, snow covered
    - Birds depend on cached food for survival
    - Stores ~30,000 nuts
    - Retrieves 90% of the seeds over a 9 month period
- Scrub Jay
    - Relayed to nutcracker

    - Lives at lower altitude where there is a milder winter
    - Caches up to 6,000 seeds (note: 1/5 of the nutcracker) and stores them for ~1 month (note: 1/9 as long as the nutcracker)

- Pigeons
    - Do not store food

Spatial Memory in Birds

- Bird puts food in cups and then wait a day
- Researchers see if, on the following day, the bird remembers where (which cups) it stored that food.

Results on memory performance:

- Clark's Nutcracker > Scrub Jay > Pigeons

Other Memory Task

- Food stores not better at non-memory task than non0food stores (delayed response task)
- Relaying in hidden food selective for selective tasks

In mammals: hippocampus is important for spatial memory

- Birds have a **hippocampal formation**
- *Their hippocampus is in a different location compared to mammals*

Conclusion:

- Ecological pressure lead to changes in its neuroanatomy

How to Minimize Costs?

- Chickadees also cache food
- Store food only in the winter
- Their hippocampal formation increases in size in the fall/winter
    - Neurogenesis
- Begins to regress in late winter
- Reduces standing cost of brain
- Possibly driven by low food availability in the winter

- Both bees (mushroom bodies(birds (chickadees) increase only those brain parts needed for task
- Supports notion of **modular** brain.

Selection for improved information Processing

- Increased number of neurons assumed to increase cognitive power
- Benefits of increased information processing must out weigh costs
- Example of selection for a larger brain

Cephalopods (naturalist-like animals) vs. Fish

- History: gradually lost to fish since the cretaceous period (about 60-70 million years ago)
    - Why?
- Naturalist-like animals dominated the sea in the Paleozoic period
- Rise of competitor (fish) in the late Paleozoic period…
- Fish took over from naturalists…
- Naturalists that survived against fish due to brain development
- To be continued next lecture…