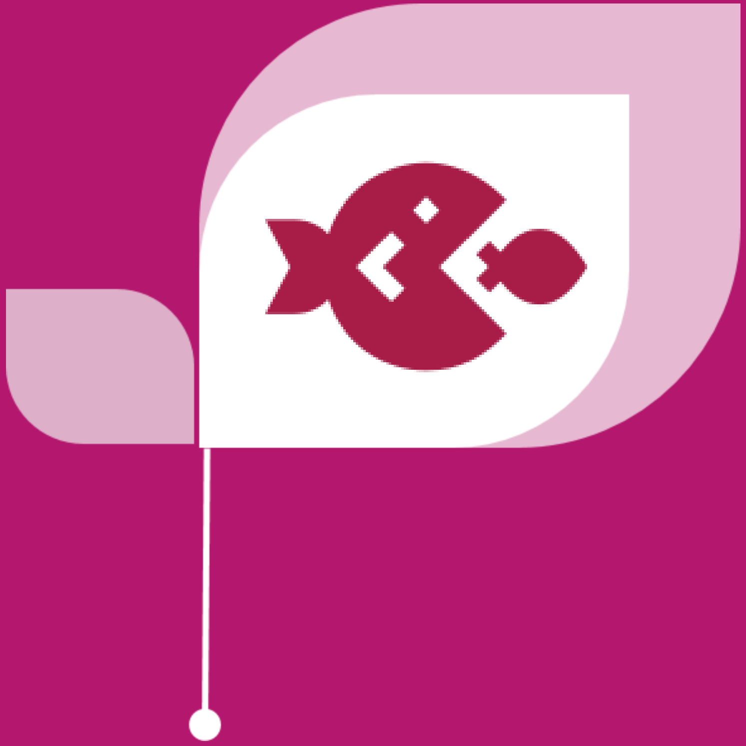


Chapter 6
Behaviour

Overview

Behavioural ecology is the study of behavioural interactions between individuals within populations and communities, usually in an evolutionary context. It looks at how competition and cooperation between and within species affects evolutionary fitness.

Behavioural ecologists look at the responses of animals to their environment from an evolutionary perspective- examining animal behaviours as adaptations that maximize the probability that an individual will survive and reproduce, and assessing the influence of genetics and environment in the development and expression of behaviour. They ask questions such as "how did this behaviour evolve? How does this behaviour contribute to survival and reproduction?"

In this chapter we will consider a wide variety of behaviours as the product of evolution.

Some of the concepts addressed in this chapter link closely with those in other chapters- particularly population and community ecology, and the evolution of adaptations. As mentioned before, the different subdisciplines of ecology are all related and overlap!

Contents

6.1

Social organisation

Sociality

Starlings flocking at dusk, trails of ants winding up a tree, herds of cows grazing in a field: as anyone will observe on a quick walk through the countryside, many of the animals familiar to us are not acting alone, but living, feeding and travelling in groups.

In ecology, this is known as **sociality** and it is the degree to which individuals in a population tend to associate in social groups and form cooperative societies.

Sociality

Sociality is adaptive; and according to behavioural ecology theory, it evolves when the net benefits of close association with individuals of the same species (conspecifics) exceed the costs. In other words, associating with others is beneficial to your survival and increases your reproductive fitness.

Studies of sociality and social behaviour are central themes in behavioural ecology: and determining fitness benefits for individuals participating in social behaviours is fundamental to understanding the evolution of animal social organization.

As you might expect, the nature and relative magnitude of the benefits and costs of sociality vary across species and environments. As a result, different levels of sociality exist.

Solitary living

Solitary species are those where individuals mainly live alone and are independent of each other, with possible exceptions for mating and raising their young. As all animals interact with other members of their species (conspecifics) at some point in their life, solitary living is not contrary to social, rather it is in contrast to cooperative behaviour. A carnivore is considered solitary if it meets with conspecifics to mate, but never cooperates to rear young, forage or defend against predators.

Solitary species exhibit limited sociality because they derive greater fitness benefits from avoiding other members of the same species. This is often to avoid competition against other members of their own species: in some species, such as striped mice, reproductive competition is a major force favouring solitary living.

As a result, solitary animals are often territorial, exhibiting aggressive displays in the presence of conspecifics. Exceptions to this will be when caring for offspring or for mating.

The great horned owl, *Bubo virginianus*, a solitary species

Solitary living

Solitary living is commonly seen in carnivores- it is estimated that the majority of carnivore species (80-95%) are solitary, including bears, jaguars, tigers, mongooses, wildcats, bobcats, pine martins, raccoons, leopards and weasels. Almost all reptile species are also solitary, as well as many insectivorous species (e.g. pangolins, hedgehogs, shrews, opossums, nightingales, anteaters), and other terrestrial herbivores and omnivores (e.g. giant and red pandas, rhinoceros, koalas, moose; sloths). Examples among invertebrates include preying mantis, ticks, mosquitos, and carpenter bees.

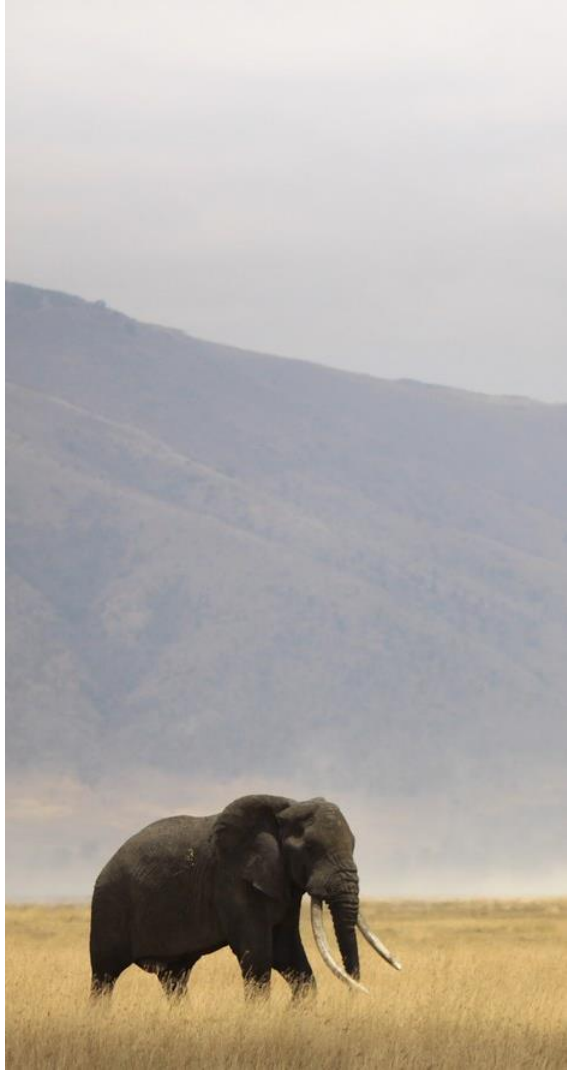
Solitary living

Research into the evolution of social behaviour amongst solitary species has been largely ignored in favour of group-living species. Because solitary species have received so much less attention in behavioural studies than group-living ones, surprisingly little is known about the social organisation of many so-called ‘solitary’ species and their interactions with conspecifics. However, it is now known that some species previously considered as solitary have in fact complex social organizations and structures.

In fact, solitary behaviour may vary considerably within a species, depending on environmental conditions, or it may be partitioned in some way.

For example, adult elephant males tend to be solitary except during mating season, while female elephants are highly social. Cheetah (*Acinonyx jubatus*) males form coalitions whereas females are solitary, and coati (*Nasua nasua*) males are solitary but females form tight social groups.

It is most likely that ‘group-living' and ‘solitary' represent two ends of a spectrum with ‘solitariness’ relating to few direct interactions between conspecifics, while still allowing for an underlying complex social system.



Gregariousness

Social, or gregarious animals are those that gather into groups to form cooperative societies with social strategies that provide shared benefits, such as predator avoidance, group defense against threats, cooperative foraging, and shared parenting. Under this definition, most vertebrates are gregarious to a certain degree. They tend to form groups (shoals, flocks, herds, packs, parties or colonies) of conspecific individuals.

Note that definitions of sociality do vary among authors. Some describe gregarious species as those that gather into a group but do not share any parental labour, such as wildebeest or atlantic cod.

Presociality

Various frameworks for describing degrees of sociality have been developed and proposed, largely in the context of **invertebrate socio-ecology,** which has been extensively studied.

Pre-sociality is a term used to describe societies which exhibit a combination of one or two, but not all 3 traits required to be **eusocial** (the highest form of sociality: see next slides). That is, individuals of the same species cooperate in caring for the young; there is division of reproductive behaviour; and there is generational overlap, so that offspring can assist parents during some period of their life.

Pre- sociality is often seen as part of an evolutionary pathway between solitary living to eusociality. Sometimes presociality is used to describe the degree of sociality observed in many mammals and birds (such as humans and chimpanzees), but because of its focus on the presence or absence of eusocial traits, this terminology is most commonly employed by invertebrate socio-ecologists.

Presociality itself is divided into subcategories: **Subsociality** and **Parasociality**: which itself subdivided into communal, semisocial and quasisocial.

Presociality

Subsociality

In subsocial taxa, there is no caste system or cooperative care of young, no cohabitation of adults, but parents care for their young for some length of time. Subsocial insects aggregate or have division of labour, or care for eggs or young. Examples include cockroaches, crickets, earwigs, mantids and spiders.

Parasociality

This includes cohabitation and sometimes cooperative behaviors, division of reproductive labour but no overlapping of adult generations.

- **Communal:** here, organisms socialize in a single, cooperative dwelling. In a communal group, adults cohabit in a single nest site, but they each care for their own young. An example are the tent caterpillars of the genus *Malacosoma.*

- **Semisocial:** semisocial behaviour involves individuals of the same generation sharing a nest and cooperating in brood care. However, it also includes division of reproductive behaviour, with a worker caste caring for the young of the reproductive caste. An example are the paper wasps of the vespid subfamily Polistinae

- **Quasisocial :** quasisocial behaviour involves individuals of the same generation sharing a nest and cooperating in brood care. Quasisocial behaviour has been observed in some Hymenoptera and spider taxa. The orchard bee, *Osmia lignaria* is another example.

Eusociality

This is the highest level of social organisation that involves complex behaviours such as group decision-making. It is found most commonly in arthropods: notably the order Hymenoperta (that include ants, bees and wasps) which contain the largest group of eusocial animals. Eusociality is considered the highest level of social organisation and is the subject of intense research.

Eusocial animals all share the following characteristics:

- Adults live in groups
- Care of young is cooperative, where individuals care for broods that aren’t their own
- Generations within a colony of adults are overlapping

Eusociality also exhibits reproductive division of labour where not all individuals get to reproduce. This is otherwise termed as a **caste system** of reproductive and non-reproductive individuals.

In **primitive eusociality** there is no morphological difference between caste members. In **advanced eusociality** organisms may have different morphologies for reproductive and non-reproductive individuals and even specialization within the non-reproductive.

Eusociality

Nearly all ant species are eusocial, as well as many bees and wasps, such as the wasp subfamilies Vespinae, the 250 species of bumblebee (Bombus spp.), the 7 species of honeybee and approximately 500 species of stingless bees (tribe Meliponini).

In total, eusocial insects are thought to comprise 75% of the world's insect biomass. Eusociality among mammals, however, is very rare, with notable exceptions including the naked mole rat *Heterocephalus glaber* and Damaraland mole rat *Fukomys damarensis*

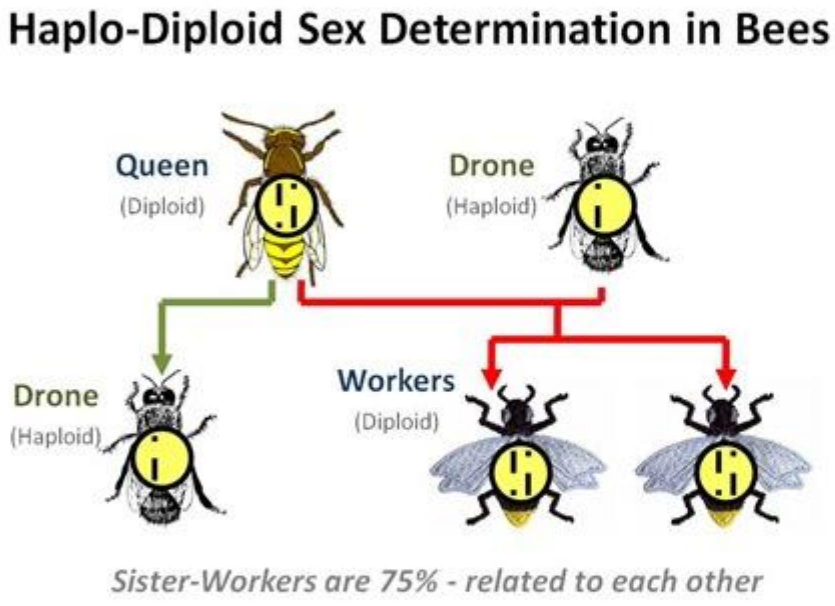
It is thought that eusociality has evolved independently multiple times across diverse terrestrial taxa and is much more common in terrestrial than aquatic environments.

Relatedness and origin of eusocialtiy

The evolution of eusociality is linked to genetics. Many eusocial insects, including ants, bees, and wasps, are **haplodiploid** (See Chapter 2). Males develop from unfertilized eggs and are haploid, whereas females develop from fertilized eggs and are diploid.

Therefore, each female has two alleles at a locus, while each male has only one. This leads to a different kin relatedness compared to **diploid** species (such as mammals). For example, a diploid female is related to her sister by 0.5, whereas a haplodiploid female is related to her sister by 0.75. A diploid individual is related to their mother by 0.5, for a haplodiploid this is 1.

Because haplodiploid species have a higher relatedness to their relatives, this lead to differences in their display of **kin selected behavior**. For example, eusocial females are expected to prefer to help their mothers raise their sisters, increasing their indirect fitness, rather than concentrating on increasing their direct fitness by raising their own offspring.



Source: http://siencebiology.blogspot.com/2011/02/haplodiploidy.html

6.2

Group living and cooperation

Group living

A murder of crows, a convocation of eagles, a bask of crocodiles, a conspiracy of lemurs: such is our innate fascination with group living that the English language provides us with a rich vocabulary of collective nouns for animal species, many of which reflect the behaviour and character of the species described.

Living together may be beneficial in many ways. One obvious benefit for social aggregations is defense from predators (see Section 6.6). For example, Musk-oxen that form a passive defensive circle when threatened by a wolf pack are much less vulnerable than an individual facing the wolves alone.

Large herds, such as wildebeest do suffer social costs from aggregating in groups — grazing sites may not provide adequate food for every individual in the group, for example. However, it is not difficult to imagine that the costs of social aggregation are much smaller than the benefits of the defense against predation. This is a simple example of how the costs and benefits of social behavior may evolve and be maintained.

Living in groups therefore involves a balance of conflict and cooperation, which is mediated by the costs and benefits associated with living socially. When the benefits of living socially exceed the costs and risks of social life, scientists predict that **social cooperation** will be favoured.

Altruism

Altruism is defined as an act by an individual that enhances the reproductive fitness of another individual, at a cost to its own fitness.

Altruism is most often seen in kin relationships, such as parenting. However, altruism may also be seen in wider social groups, where animals sometimes behave in ways that reduce their individual fitness but increase the fitness of other individuals in the population. One example is ground squirrels, who may warn other members of their group about a predatory hawk overhead. This brings the hawk's attention to the individual giving the warning call. This risky behaviour benefits other individuals in the squirrel's group.

The benefit of an altruistic behaviour is ultimately measured in its effect on an animal's lifetime reproductive success. Altruism by definition decreases the fitness of the individual, but natural selection operates against individuals who reduce their own fitness. So how could patterns of altruism evolve? Evolutionary biologists and animal behaviourists have long sought to identify the mechanisms that can explain the "problem of altruism."

The solution comes from decades of research into genetics and animal behaviour, which has taught us that altruism is a powerful demonstration of natural selection at work.

Group Selection

One theory to explain altruism is **Group Selection**. This states that natural selection will act at the level of the group, so that groups containing altruistic individuals will be more likely to survive than those without.

However, with the exception of social insects, the Group Selection theory has largely been debunked, because it is accepted that natural selection acts on the individual, and it is the individual's fitness that drives evolution. In order to be favoured by selection, the gene causing the altruistic behaviour has to benefit from the altruistic behaviour.

Kin selection

An alternative to the group selection theory is the **kin-selection** theory. This states that it is as advantageous to help with the upbringing of full sibs as it is to produce and raise one's own offspring. Kin-selection allows an individual to increase the success of its genes by helping relatives that share those genes. The reproductive success of a relative’s offspring is favoured, even at a cost to the organism’s own survival.

According to **Hamilton's rule**, kin selection causes genes to increase in frequency when the genetic relatedness of a recipient to an actor multiplied by the benefit to the recipient is greater than the reproductive cost to the actor.

Reciprocal altruism

While kin-selection helps understand altruism among relatives, it does not explain altruistic behaviour between unrelated individuals.

The concept of **reciprocal altruism** addresses this. It states that an organism may perform an altruistic act towards another individual that temporarily reduces its own fitness, if the expectation is that the other individual will perform a reciprocal altruistic act in a similar manner at a later time. Conditions for reciprocal altruism are :

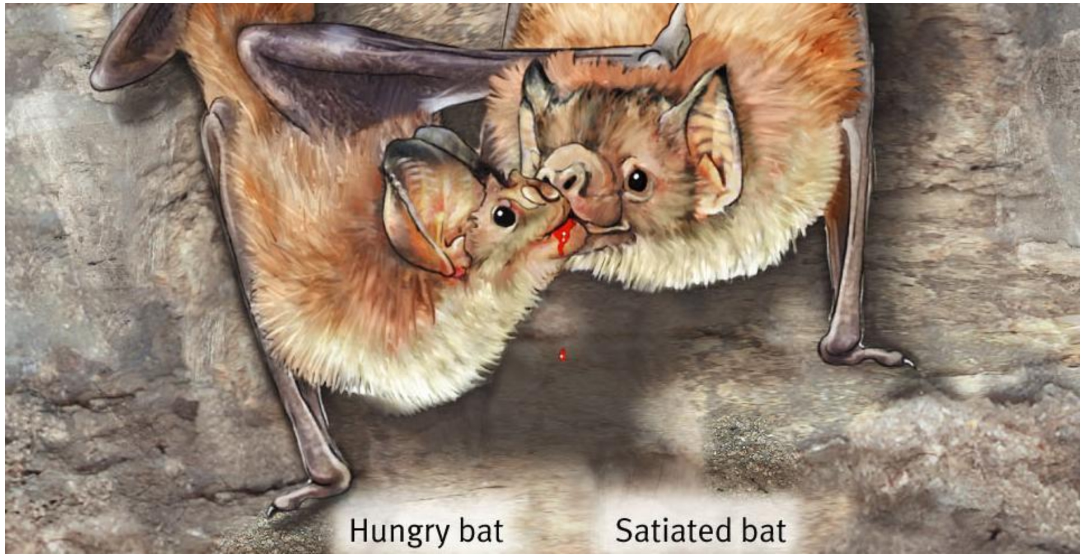
1. the behaviour must reduce a donor's fitness relative to a selfish alternative
2. the fitness of the recipient must be elevated relative to non-recipients
3. the performance of the behaviour must not depend on the receipt of an immediate benefit
4. conditions 1, 2, and 3 must apply to both individuals engaging in reciprocal helping

Reciprocal altruism

A good example of reciprocal altruism is seen in Vampire bats. In Costa Rica, Vampire bats returning from an unsuccessful foraging bout will beg to share blood meals wiith successful individuals, who will often agree.

However, bats do not share their meals with all other bats equally. Research has shown that the bats are far more likely to share blood with bats they are more likely to encounter in the future. In other words, when there is a greater opportunity for reciprocation, the bats are more likely to share their meals. Bats do not share blood meals with other bats if there is little chance that the other individual will be able to return the favour.

Reciprocity enables the existence of altruism because — in the long term — the benefits of altruism can outweigh the costs of altruism. In this particular example, the relative cost of sharing food, when available, is less than the potential future benefit of receiving food when hungry.



6.3

Mating systems

Mating systems

Animals often choose their mates with a great deal of care- mate choice is important for an individual to maximise their reproductive success. Different species have evolved different strategies for choosing mates—resulting in considerable diversity among animal species in their mating patterns.

Mating systems describe the way a social group is structured in relation to sexual behaviour, in particular how males and females pair when choosing a mate.

Mating systems are important to understand because they reflect the result of natural selection on mate choice, and ultimately on strategies for maximizing individual reproductive success.

Furthermore, males and females differ greatly in the investment each one makes to reproduce, and so they often have very different approaches to mate choice.

Types of mating system

In the next few slides we will look at the different kinds of mating system that are recognised in the animal kingdom. All of these mating systems lead to different mate choice outcomes and thus these systems affect how sexual selection works in the species which practice them.

In general, mating systems are described as either **monogamous** (animals that have only one reproductive partner) or **polygamous** (animals that mate with mutliple partners). Within polygamy, three types are recognised: polygyny, polyandry and polygynandry.

Monogamy

Monogamy is rare in mammals, occurring in only 3-9% of species, but very common in birds (about 90%). Monogamy might be short-term, lasting for one or two mating seasons, span many years, or may be life-long. Two kinds of monogamy are recognised: social monogamy and genetic monogamy.

Social monogamy refers to the co-habitation of one male and one female. The pair cooperates in search of resources such as food and shelter, or parental care. However, while they co-habit, sexual fidelity is not necessarily practiced, and both males and females may seek extra-pair copulations (or EPCs).

Genetic monogamy is where you get sexual fidelity of the bonding pair. However, this practice is seen in individual pairs, but no one species has been shown to be fully genetically monogamous.

In fact, most birds practice social monogamy rather than genetic monogamy.

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Albatrosses and dik-diks, examples of monogamous species

Polygyny

Polygyny is a form of polygamy where one male has exclusive access to multiple females, but females only mate with a single male.

It is associated with one-male, multi-female groups, and many systems where there is an ‘alpha male’. It is common in mammals, such as western lowland gorillas, elephant seals, red deer, Bengal tiger and elk, and is seen in some birds, e.g. Redwinged blackbirds.

Polygyny

Different kinds of polygyny are recognised:

Resource-defense polygyny

This is where one male acquires several females by controlling a resource that females are attracted to. Males that provide more resources or defend better territories attract more females. The cost of this for females is in sharing resources with other females that the male has attracted.

Examples include red-winged blackbirds and damselflies. Male black-winged damselflies wait for females to come to them, defending territories that contain the kind of aquatic vegetation in which females prefer to lay their eggs.

Polygyny

Female-defense polygyny

This is where one male directly defends several females against conspecifics to monopolise access to them. Females form the stable core of the group, and the female 'puts up' with other females because of the male's resources.

An example would be Bighorn sheep whose rams congregate at areas where potential mates are and then fight with other males to monopolize females.

Polygyny

Lek polygyny

This is where groups of males gather together to form competitive displays to attract and entice visiting females, who are surveying prospective partners. The lek mating system is uniquely driven by the females' pursuit of their mate, rather than the males`. Leks are commonly formed before or during the breeding season.

Examples include sage grouse, stalk-eyed flies and birds of paradise.

Polyandry

In polyandrous systems, one female has an exclusive relationship with two or more males. Polyandry is associated with multi-male, single-female group compositions. It occurs where there are direct benefits for females allowing fertilization assurance, provision of resources, and parental care for their offspring.

It is common in insect species (e.g. Western Honey Bee*,* field cricket and the red flour beetle) and seen in other invertebrates (e.g. the spider *Stegodyphus lineatus*) and fish (e.g. pipefish). Polyandry is rare among mammals, but is the dominant social structure in the New World monkey family Callitrichidae. Other mammalian examples include broat-footed marsupial mice and bandicoots. It is rare in birds (about 1% of bird species are polyandrous, e.g. jacanas and dunnocks) but prominent in reptiles, especially tortoises.

Polygynandry

Polygynandry is where multiple females and males mate with each other, and males may care for the broods of several females. It allows groups of males and females to live together and spend less time being concerned with mate competition.

Polygynandry may be advantageous from the female's perspective because it causes paternity confusion, which decreases infanticide and allows her to have multiple males care for her brood.

Polygynandry is common in nature. Examples include European badgers, red fox, African ground squirrel, some birds (e.g. dunnocks); and some fish (e.g. bluegills. Cichlid fish, dusky pipefish)

Promiscuity

In **promiscuous** mating systems a member of one sex within the social group mates with any member of the opposite sex. There are no pair bonds, and males and females often seem to mate randomly. As it is typically more advantageous for one or both sexes to pick their mate, promiscuity may occur in species for which the environment is unpredictable.

Examples of promiscuous species include chimpanzees and bonobos.

6.4

Sexual selection

Sexual selection

Sexual selection is a special case of natural selection where members of one biological sex compete with members of the same sex for access to mates. Sexual selection acts on an organism’s ability to obtain a mate – often by any means necessary.

Many organisms go to extreme lengths to obtain a mate, and sexual selection is often powerful enough to produce features that are harmful to the individual's survival, or come at a heavy cost to the individual.

Sexual selection is often characterized by intense competition between males for females, a wide variety of strategies to maximize reproductive success, exaggerated male traits and co-evolution of sexual traits in males and females.

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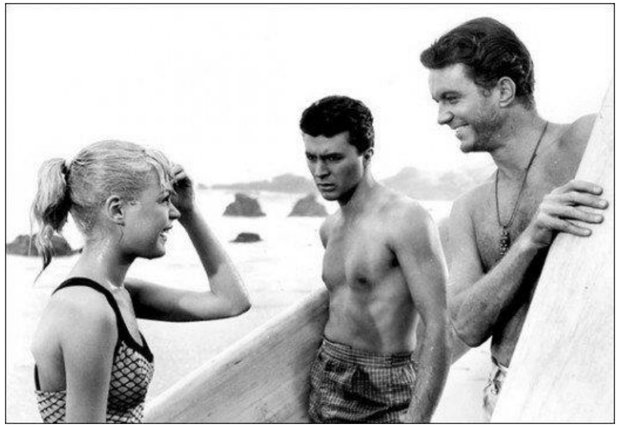
Sexual selection and reproductive success

Sex roles are determined by differences in gametes: in species with two separate sexes, females produce fewer, larger gametes than males. For example, for very human egg ovulated, about 1 billion sperm are produced!

The form of sexual reproduction that involves the fusion of gametes that differ in size and form is known as **anisogamy**, and it is common in plants and animals.

Because of this difference, female reproduction is considered to be primarily limited by access to resources to nourish and produce a few, large gametes, whereas male reproduction is limited by access to females.

This means that males typically compete among themselves for access to females, whereas females tend to be choosy and mate only with preferred males. Females almost always invest more energy into producing offspring than males, and therefore, in most species, females are a limiting resource over which the other sex will compete.



Bateman’s principle

This is known as **Bateman’s principle**, which states that since males are capable of producing millions of sperm cells with little effort, females invest much higher levels of energy in order to nurture a relatively small number of eggs. The female therefore plays a significantly larger role in their offspring's reproductive success.

Bateman's principle goes further, postulating that **variance** among females in mating success should be low, whereas variance among males in mating success should be high. This stems from the fact that by mating once, females should be able to fertilize all their eggs whereas in males, reproductive success is based on the number of times they have mated.

A successful male can potentially sire many offspring. If a male gains a disproportionate share of reproduction, he will take away reproductive opportunities from other males, leading to a high reproductive variance among males.

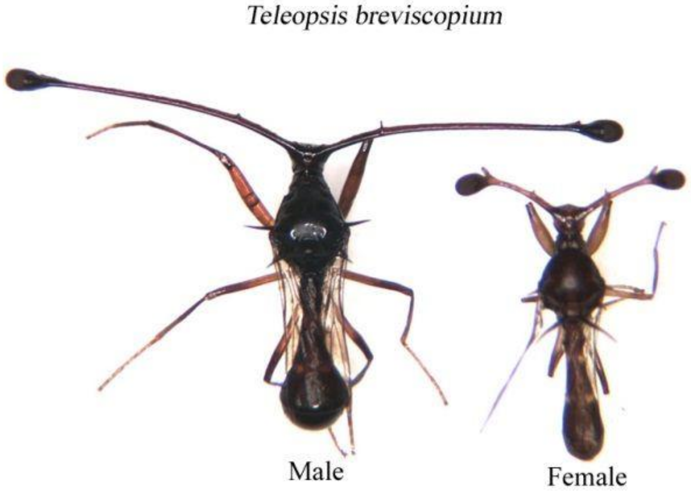
A successful female, on the other hand, is limited in the number of offspring she can produce. She will not take away reproductive opportunities from other females, leading to a smaller variance in reproductive success.

The higher the reproductive variance, the stronger the effects of sexual selection.

Sexual dimorphism

Strong sexual selection typically results **in sexually dimorphic traits** that are exaggerated, or more elaborate, in the sex with highest reproductive variance- usually males.

The elaborate plumage of male birds of paradise are examples of sexually dimorphic traits. Other examples include the vivid coloration, large body size and canines of male mandrills, the large, greyed body and sagittal crest of the male silverback gorilla, and the exaggerated eyespan of the male stalk-eyed fly.



Female mate choice

Because of the higher investment females make in each gamete than males, in most species, females are choosier when picking a mate than males.

Females may prefer certain males for a variety of reasons, including "good genes‟. This means that the male has attributes which predict better survivorship of the offspring, good potential parenting by the male, or possession of resources by the male that will support the offspring during their growth and development.

Female mate choice

Additionally, in most species, females are more likely to provide parental care.

Females that carefully select their mates are at a lower risk of losing their reproductive investment. Males may be under strong selection for certain traits that are favoured by females. Most females look at these traits as indicators of their partner's fitness.

Selection favours females that choose males that enhance the likelihood of her offspring's success. For example, female western lowland gorillas choose males that will best protect their offspring from the infanticidal behaviour of other, competitive males. Research has shown that bigger, more muscular silverbacks are in fact, more effective at attracting females than smaller ones.

Males with more elaborate ornamentation, or that are more colourful, can also display a good indicator of value as a mate, and may win the chance to mate with a particular female.

Male mate choice

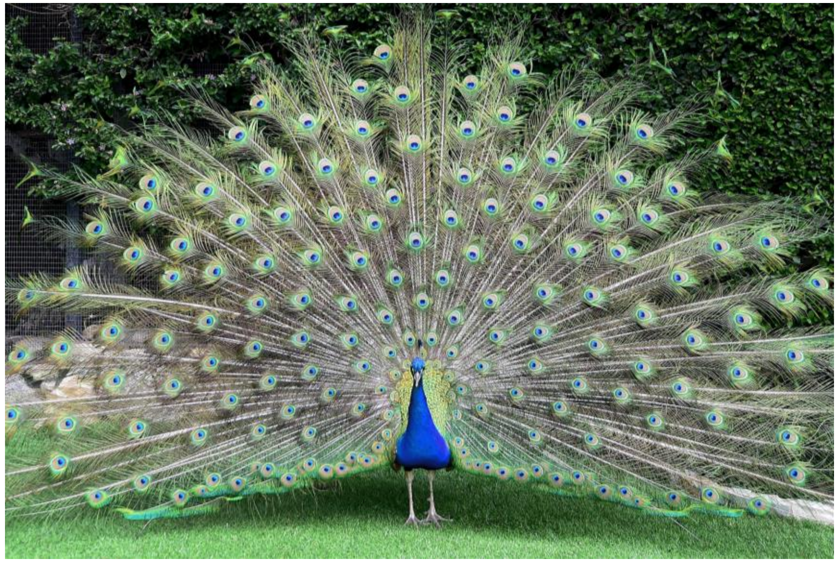
The importance of male mate choice is controversial. Older theory predicts that male mate choice should be less common in animals. However it plays an important role in many mating systems, and the cost of mating for males may have been underestimated in earlier studies.

Male mate choice occurs most often when males are substantially involved in caring for their offspring, or when there is great variation in the quality of the females as mates within a population. If males are choosy about their mate, then over time females may evolve ornamentation or coloration that is subject to sexual selection (see next slides).

Parental care

Most species provide little or no care to their offspring, but in species where parental care is required, variance in reproductive success will be impacted not only by fertilization success, but also by the contribution of each sex to the care of the offspring. In this way, parental care can also contribute to sexual dimorphism.

For example, if females provide more parental care than males, the variance in male reproductive success can be expected to be large, since females that care for offspring will not be immediately available for further reproduction and competition for available females will increase among males. Here, we expect to see exaggerated secondary sexual traits in males, such as the extraordinary tail feathers of peacocks. Exaggerated sexual dimorphism is commonly seen in polygamous mating systems.



Parental care

In contrast, in species where biparental care is required to successfully raise offspring, the variance in male reproductive success is generally lower, since males that are engaged in providing parental care will not be able to invest as much energy in pursuing additional mating opportunities. This situation often results in the emergence of sexually monomorphic species, in which the male and female look and behave in similar ways (e.g. boobies). This is commonly seen in **monogamous** mating systems.

Rarely, only males provide parental care, and here males can become the limiting resource for females. Under these circumstances, the variance in reproductive success may be high for females who then tend to monopolize access to one or more males to care for their offspring. Males may then become choosy about which females they mate with. This often results in reversed sexual dimorphism, such that females evolve more elaborate secondary sexual characters than males, and is often seen in **polyandrous** mating systems. An example is the red-necked phalarophe, where the female is bigger and more aggressive than the male.

6.5

Foraging behaviour

Foraging behaviour

Foraging is searching for wild food resources. It is one of the most important animal behaviours because it directly affects an animal's ability to survive and reproduce, and therefore its fitness.

Foraging theory is a branch of behavioural ecology that studies the foraging behaviour of animals in response to the environment where the animal lives.

Several factors affect an animal's ability to forage and acquire profitable resources: this includes learning, genetics, predators and parasites.

Types of foraging

Foraging can be categorized into two main types: solitary and group foraging.

Solitary foraging occurs when animals forage alone. They may exploit a patch of habitat manually or use tools, such as chimpanzees fishing for termites with a stick. Because foraging incurs a cost itself in terms of time and energy, models have been developed to understand how an animal behaves when foraging.

Optimal foraging theory (OFT) is used to understand solitary foraging. To maximize fitness, an animal adopts a foraging strategy that provides the most benefit (energy) for the lowest cost, maximizing the net energy gained. OFT helps predict the best strategy that an animal can use to achieve this goal.

A tiger stalking prey is an example of solitary foraging

Crab-eating macaques (*Macaca fascicularis*) use stone tools to crack open shellfish- another example of solitary foraging

Types of foraging

Group foraging occurs when animals forage together- here, success depends not only on your own foraging behaviours but the behaviours of others as well. Animals may be seen foraging together when it is both beneficial and detrimental for them to do so.

Group foraging brings both costs and benefits to the members of that group: for predators benefits include being able to capture larger prey and more difficult prey; for prey this includes reduced predation risk. Costs include competition for resources with other group members.

The ideal free distribution is used to understand group foraging. This states that the number of individuals that will aggregate in various patches is proportional to the amount of resources available in each patch.

As group foragers, lionesses make hunting decisions based on obtaining food, territory defense and protecting young

Territoriality

When foraging, animals often move over large areas- the area an individual or group uses regularly to forage iis called its **home range**. Home ranges within species may overlap, e.g. for western lowland gorillas.

When an individual or group defends a portion of his home range and uses it exclusively, this is known as its **territory.**

Most vertebrates and some invertebrates, such as arthropods, including insects, exhibit **territorial behaviour.** Possession of a territory involves **aggressive behaviour** and thus contrasts with the home range. A critical aspect of territorial behaviour is defense against intrusion. Animals use displays to advertise that territories are occupied, for example a robin singing from a perch to prevent territory invasion by a neighbouring bird.

The type of territory varies with the social behaviour and environmental and resource requirements of the particular species and often serves more than one function. In selecting a territory, the size and quality play crucial roles. Several types of resource in a territory may be defended: this could be food, nests, offspring, or mating opportunities. Whatever the type, the territory acts as a spacing mechanism and a means of allocating resources among a segment of the population and denying it to others.

Territoriality has its costs, as displays use energy and attacks could lead to injury. Benefits include increased food access. The cost-benefit trade-off needs to be economically affordable. This will depend on resource availability: if the resources deplete rapidly, do not renew rapidy and are unpredictable in space and time, then it is unlikely to be economically defendable. However if the resources renew rapidly and are predictable in space and time, then it is more likely to be economic to defend

6.6

Anti-predator behaviour

Anti-predator behaviour

Most animals face predation pressure and must avoid or defend themselves against predators in order to survive and successfully reproduce – this is an important determinant of **fitness**.

In addition to physical traits such as armour and camouflage, animals use behaviour to avoid and survive predation.

Prey can either use **general** cues to detect the presence of a predatory threat, or **species-specific** cues to identify a predator's identity and determine its motivation and therefore the most appropriate behavioural response.

Encounters with predators can result in death; therefore, many animals focus their antipredator efforts on **avoiding** and **preventing** encounters. However, vigilance can carry costs including energetic expenses and time unavailable for searching for food or mates. As a result, an animal's antipredator behaviour is designed to minimize its costs and maximize its effectiveness for surviving predation.

Predator detection

The ability to detect predators is an essential part of antipredator behaviour. This can be innate, for example, animals can identify predators as a threat even if they have never encountered them before, or learned after exposure to a predatory threat.

Animals can respond to general cues, such as a sudden movement, or to specific cues, such as odour or sight. Prey can rely on a variety of sensory modes to detect these predator cues, including visual, chemical, auditory, and tactile senses.

Predator avoidance

After an animal has determined that a predator is nearby, it must then take action to avoid encountering this threat. Encounters are most easily avoided by preventing predators from detecting them in the first instance. One effective strategy is by avoiding habitat occupied by predators, or being active at different times of the day. Animals can also avoid attracting a predator's attention by minimizing cues of their presence, such as by remaining silent, seeking refuge, disguising themselves or reducing activity levels when risk of predation is high.

Predator avoidance

Staying out of sight

Animals may avoid predators by living out of sight of them, or by being active at different times of the day. This includes **nocturnality**, living underground (e.g. in burrows) or living in caves. Nocturnality and subterranean life are all behavioural forms of detection avoidance by **crypsis**. Examples include the nocturnal foraging behaviour of fruit-bats, the burrowing of cape ground squirrels, and the cave-dwelling fish *Poecilia mexicana*.

Predator avoidance

Camouflage

Many animals avoid predators through effective camouflage. This can be through the adoption of any combination of materials, colouration or light to either make the prey less detectable (**crypsis**), or by disguising them as something else (**mimicry**).

Most camouflage methods involve crypsis. Some animals' colours and patterns resemble their background, such as the peppered moth, whose colouration was famously shown to have undergone natural selection in the 19th century to match the changing colour of tree trunks in polluted urban areas.

Some species use disruptive colouration (e.g. spots or stripes) that break up their outline, making them less visible- examples include zebras and leopards. Others, such as bushbuck, use distractive markings with high contrast that serve as camouflage by distracting the predator's attention from recognising the prey as a whole. Others, such as decorator crabs, camouflage their bodies by covering themselves with vegetation or stones: this is known as self-decoration.

Predator avoidance

Masquerade

Sometimes animals can hide in plain sight by imitating inedible, non living objects. This is a form of mimicry known as masquerade. The difference here compared to crypsis is that the appearance of cryptic prey make them difficult to detect, whereas the appearance of masquerading prey ensures that predators mistake them for inedible objects once they are detected.

Larvae of the early thorn moth *Selenia dentaria* masquerade as twigs

The Ghost mantis *Phyllocrania paradoxa* masquerades as a dead leaf

Cuttlefish can change their appearance to resemble rocks and seaweed

Predator encounter

Sometimes an encounter with a predator is inevitable, and to deal with such situations there are many strategies that animals have evolved and can employ to ward off an attack and improve their chances of survival.

Predator encounter

Pursuit deterrant signals

Upon an encounter with a predator, some prey species will send behavioural signals to indicate enhanced fitness and convince the predator that pursuit is not worth the effort. This is done by communicating, for example through loud vocalisations or displays, that the predator has already been detected, that the prey has a high level of fitness and that it will most likely outrun the predator. This is considered an intimidation strategy.

Examples include gazelles ‘stotting’- this is where they jump high in the air when chased, lifting all four feet off the ground simultaneously. Spot nosed guenons produce distinct alarm calls that signal to eagles and leopards they have been detected, some lizards do push-up displays and tail wags. Prey that live in large groups can intimidate a predator by simultaneously mobbing it, driving it away before it can attack, e.g. crows mobbing a bird of prey.

Predator encounter

Escape (flight)

Fleeing a predator is a standard prey reaction, often by any means available. Erratic escape paths may be employed to confuse the predator. This tactic is useful if the predator is not too close and/or there is a refuge nearby, and the chance of the prey escaping is high.

Self-amputation- or **autotomy**- is a last-ditch attempt to escape an attacking predator. This is seen in species that are capable of regeneration, such as sea slugs, crabs, lizards and geckos, that may shed a tail or claw that can be regrown.

Predator encounter

Aposematism

Animals that warn predators of their dangerous nature are called **aposematic**. These are considered honest signals, because the animal is advertising a real danger, in that it is poisonous or toxic. Aposematic warning signals are commonly presented as vivid colouration, but may come in other forms. For example the lionfish advertises its venomous spines with spiky fin rays and showy pectoral fins, and the rattlesnake uses its rattle to scare off potential predators. Research has shown that vertebrates associate red, orange, yellow and white as signs of danger, and many unpalatable prey species have evolved colour schemes that reflect this. Many butterflies have aposematic coloration, bitter taste, and poisons in their body that are toxic to most vertebrates. In return, many predators have an innate avoidance response to aposematically coloured prey items.

Predator encounter

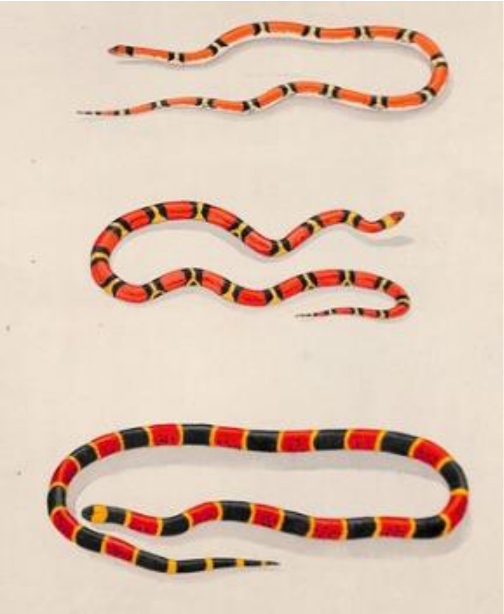
Mimicry

This occurs when one organism mimics properties of a second, to confuse a third. There are two classical types of defensive mimicry: Batesian and Müllerian. Both involve aposematic colouration or warning signals to avoid attack.

In Batesian mimicry a harmless species has evolved to imitate the warning signals of a harmful species that has chemical defences. In Müllerian mimicry two or more harmful species develop similar appearances as a shared protective device. This increases the chances that a predator will avoid all animals with a particular color or pattern.

An example of Batesian mimicry: mimetic forms of female *Papilio dardanus* (right) mimic unpalatable butterfly species in the family Danaidae (right)

Müllerian mimicry: Scarlet Snake *Cemophora coccinea*, Scarlet King Snake *Lampropeltis elapsoides* and Coral Snake *Micrurus fulvius*, all share similar banding patterns



Predator encounter

Diematic behaviour

Diematic behaviour or markings have the effect of startling or frightening potential predators, and are carried out by prey species that lack strong defenses. In this sense they are considered deceptive or ‘bluffing’ behaviour.

A common form of diematic defence are conspicuous eye-spots, seen in moths, butterflies, mantises, octopuses. Usually these take the form of a pair of false-eye markings which can frighten away a predator, or at least startle it long enough for the insect to make it's escape.

Diematic mimicry is a common form of defence in caterpillars as well as in adult butterflies and moths. For example, snake mimicry is seen in the giant Atlas moths. In these species the forewing apex resembles the eyes and mouth of a snake. When threatened, the moth will drop to the floor and writhe around, slowing flapping its wings to imitate snake head and neck movements and scare away predators.

Predator encounter

Apparent death

Feigning death – or **thanatosis**- is another deceptive behaviour that some species exhibit as a predator defense mechanism.

The Virginia opossum and the hog nosed snake (*Heterodon* spp.) are commonly cited examples of defensive thanatosis, where upon detection of a predator threat, the animals play dead by assuming contorted postures with their eyes open and their tongues protruding from gaping mouths.

Predator encounter

Chemical defense

Many animals and plants use chemical toxins for self-defense and to fight back in the face of an attack. They may be stored in glands or spines, or the animal may eject noxious substances to actively deter predators. Bombardier beetles blast their attackers with a jet of boiling acid from their abdomens. Some species exhibit a phenomenon known as autohaemorrhaging: African armoured ground crickets expel toxic blood from gaps in their bodies when attacked by predators, as well as regurgitating recently eaten food. Skunks, weasels and polecats emit foul smelling liquids from their anal glands, and slow lorises produce a toxin in a gland on their arm, which is activated when licked to produce a toxic bite.

Predator encounter

Defensive structures

And other animals protect themselves against predators with armour in the form of hard shells, leathery or scaly skin or tough chitinous exoskeletons.

Predator encounter

Distraction displays

Distraction displays are performed to confuse or distract a predator- this could be to give an animal a last chance to escape, or to attract attackers' attention away from an object, such as a nest or young, that is being protected.

When marine molluscs such as cuttlefish, squid and octopuses eject ink jets, this creates a cloud, obscuring the predator's view and giving them time to escape. In sea hares, a mixture of chemicals are released that also affect the predator's feeding senses, causing it to attack the cloud. This is known as phagomimicry.

Many nesting birds perform distraction displays: this is a well-known phenomenon in birds with ground nests, such as shore-birds and waterfowl. Some species feign injury or exhaustion when threatened, such as the broken wing displays of the killdeer. This is also a deceptive behaviour.

©Harold Stiver

Group living

Because there is safety in numbers, **sociality** can also be viewed as an anti-predator defense, particularly when young are threatened.

Group living

Improved vigilance

Groups of animals are better protected if groups are able to detect predators sooner than solitary individuals. Larger groups may have a greater overall vigilance than small groups due to the 'many eyes' hypothesis: in larger groups, there are more chances for an animal to notice a predator sooner and alert the rest of the group.

This has been shown in wood pigeons (*Columba palumbus*) where large flocks are more able to escape predation from goshawks because they are able to detect them and escape more rapidly than they would as solitary individuals.

Some species invest heavily in vigilance behaviour to reduce predation risk, e.g. meerkats, who forage in groups, sometimes far from their burrows and employ sentinels who scan for predators.

Group living

Dilution effect

When animals live in groups, a dilution effect is seen that reduces their risk of attack. Williams and Hamilton first proposed this idea- that animals have evolved to live in groups to ‘dilute’ the risk of predation and attack. In other words, you’re less likely to be a target if you’re not alone.

The dilution effect is an accepted explanation for many group-living taxa, such as fish. It has been shown experimentally, for example, in Camargue horses, individuals living in larger groups are attacked less frequently by horse-flies than those living in smaller groups.

Group living

Confusion Effect

Individuals living in large groups may be safer from attack if predators become confused by the large numbers of moving individuals. In the zebra, is thought that its stripes create distracting visual illusions when a herd of zebras are moving at speed together, causing confusion for predators such as lions[1].

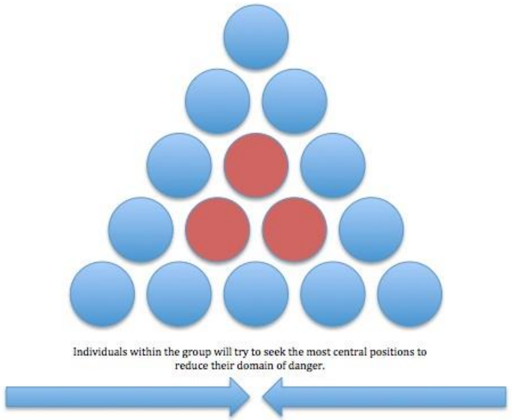
The confusion effect is also thought to explain the evolution of some swarming behaviours[2]. For example, European starlings (*Sturnus vulgaris*) form spectacular, coordinated swarming flocks of hundreds of thousands of birds (known as murmurations), and desert locusts (*Schistocerca gregaria*) form massive swarms with billions of locusts . Research suggests that the larger the flock, the harder it is for predators to single out and catch individual prey[3].

1. https://thehorse.com/111642/study-zebra-stripes-could-confuse-predators/
2. Olson et al., 2013. Predator confusion is sufficient to evolve swarming behaviour**.** *J. R. Soc. Interface. 10.*
3. https://www.sciencemag.org/news/2017/01/flocking-starlings-evade-predators-confusion-effect

Group living

Selfish herd theory

Proposed by WD Hamilton, the selfish-herd theory is a common explanation for why animals seek central positions within a group. The theory states that individuals will reduce their predation risk by putting other conspecifics between them and the predator. The prediction is that scattered individuals will form tightly packed groups when alerted to danger, and that the animals on the periphery of the group will be at higher risk of predation than those towards the centre. Thus, animals are expected to seek central positions in order to reduce their danger. The selfish herd theory has been tested and demonstrated in a number of species, including fiddler crabs, fish, and sheep.



Individuals within the group will try to seek the most central positions to reduce their domain of danger.

6.7

Evolutionarily Stable Strategies

Biological Interactions

Individuals are always interacting – interactions range from cooperative to antagonistic- and when there are limited resources conflicts can occur. This could be at the species level, such as between predators and prey, or it could be within species, such as between rivals for mates. Sometimes conflicts may be between close relatives such as siblings or parents and offspring.

Evolutionary ecologists aim to understand the complex behavioural relationships between organisms as they interact to obtain limited resources.

Interactions are costly: energy is invested in both competition and cooperation as a means to acquire a resource. The energy spent is a **cost** to the organism, and the resources are **benefits**.

The relative cost to the benefits obtained following an interaction determines the net gain or loss incurred by the organism, and this value is referred to as the **payoff**. Different strategies result in different payoffs: these interaction strategies are considered as **phenotypes** by evolutionary ecologists.

The optimal strategy for an individual is one that maximizes the expected payoff, and the organism with the best interaction strategy has the highest fitness. Since the interaction strategy (phenotype) can directly relate to fitness, the optimum strategy will be favoured under natural selection.

Evolutionary Game theory (EGT)

Since biological interactions involve two or more individuals with strategies, biologists use **game theory** to understand the evolutionary consequences of interactions.

Game theory is a branch of mathematics that investigates strategy and decision-making in social situations. It tries to determine the optimal decision-making of independent and competing actors in a strategic setting. A key part of the concept is that individual players make decisions, but the payoff to any one individual depends not only on its own strategy, but the strategies and decisions made by all other individuals involved.

In this way, interactions between biological organisms with either competing or identical strategies can be treated as games with multiple players.

Evolutionary game theory defines a framework of contests, strategies, and analytics into which Darwinian competition can be modelled.

The key insight of evolutionary game theory is that many behaviours involve the interaction of multiple organisms in a population, and the success of any one of these organisms depends on how its behaviour interacts with that of others. So the fitness of an individual organism can’t be measured in isolation; rather it has to be evaluated in the context of the full population in which it lives.

Evolutionarily Stable Strategies

An important concept of evolutionary game theory is that of **evolutionarily stable strategy** (ESS).

An ESS is a strategy which if adopted by a population cannot be invaded by any competing alternative strategy.

For a set of behaviours to be conserved over evolutionary time, they must be the most profitable pathway of action for that population, so that no alternative behaviour can invade.

In some populations, all individuals may have the same strategy phenotype (identical strategies). This will be an ESS if that strategy cannot be replaced or invaded by any other strategy through natural selection. For example, suppose that in a population of frogs, males fight to the death over breeding ponds. This would be an ESS if males that fight to the death are always more successful (in fitness terms) than the occasional cowardly frog that does not fight to the death.

An ESS must satisfy two conditions:

1) an individual employing strategy A must do better against another individual employing strategy A than any other strategy;
2) should a new strategy evolve (A') that does equally well against strategy A, for A to be an ESS, an individual employing strategy A must do better against an individual employing strategy A' than an individual employing strategy A�much

The concept of ESS was introduced and defined by John Maynard Smith and George R. Price and is central to Maynard Smith's (1982) book *Evolution and the Theory of Games*.

ESS and Nash equilibrium

In game theory the **Nash equilibrium** is a strategy in a game where if all players adopt it, no player will benefit by switching to play any alternative strategy. No player has anything to gain by changing only his or her own strategy unilaterally.

ESS is the analogous notion for evolutionary situations, where a genetically-determined strategy tends to persist once it is prevalent in a population.

The difference between a Nash equilibrium and an ESS is that a Nash equilibrium may sometimes exist due to the assumption that rational foresight prevents players from playing an alternative strategy with no short term cost, but which will eventually be beaten by a third strategy. However, an ESS assumes that natural selection is the only force which selects against using strategies with lower payoffs.

Video link

Now watch either or both of these two videos on Evolutionarily Stable Strategies:

Game Theory | Evolutionary Stable Strategies

Video 1: Systems Innovation lecture (6m 25): https://www.youtube.com/watch?v=4Hfdg3rnxnQ

Video 2: Explanation by Richard Dawkins (3m): https://www.youtube.com/watch?v=mUxt--mMjwA

6.8

Plant behaviour

Plant behaviour

Although Darwin wrote the first book on plant behaviour, most research that has been conducted into behaviour and sociality has been on animals. It was long assumed that plants cannot "behave" because they lack a central nervous system. But if behaviour is described as the ability of an organism to respond to signals in its environment and sociality means that individuals live and interact in groups, then this applies to plants too!

Research into plant sociality is still fairly new compared to animals, however, scientists have found them capable of behaviours once thought unique to animals. Like animals, plants acquire, store and process environmental information relevant to their fitness, and this is particularly evident in their decision-making.

https://www.eurekalert.org/pub_releases/2009-11/mu-ppt111609.php and https://www.wired.com/2009/11/plant-family-values/

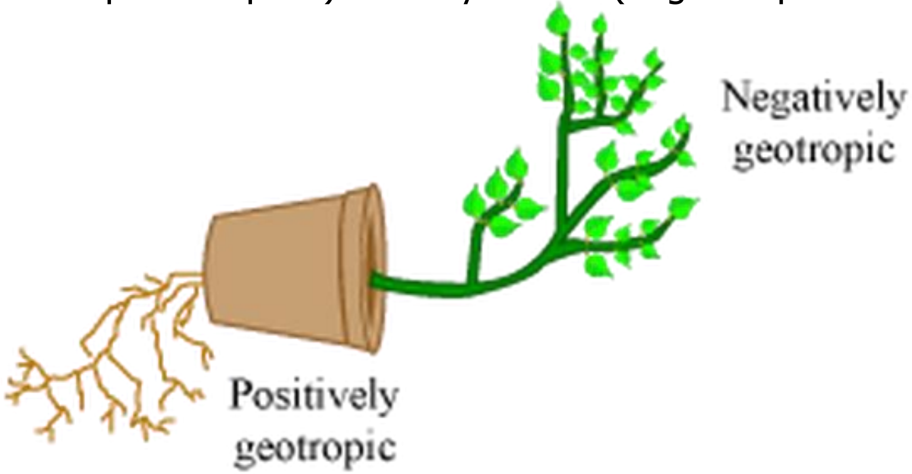
Movement

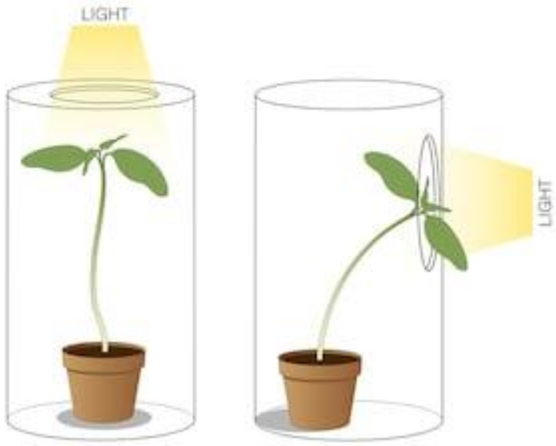
Tropism

Although usually rooted to the ground or some other matrix, plants exhibit a wide range of sophisticated mechanisms that allow them to move. The instinctive behaviour of a plant depends mainly on growth or movement in a given direction due to changes in its environment. Movements in plants are most frequently regarded as a result of action of an environmental stimulus: and the ability to grow or move toward or away from an external stimulus is known as **tropism**. There are many kinds of tropism in plants, some of which are described below:

Gravitropism describes the ability of plants to grow in response to gravity. This ensures that roots grow into the soil (positive gravitropism) and that stems grow in the opposite direction (negative gravitropism).

Phototropism is a plant's ability to reorient organ growth towards a directional light source: either towards it (positive phototropism) or away from it (negative phototropism).



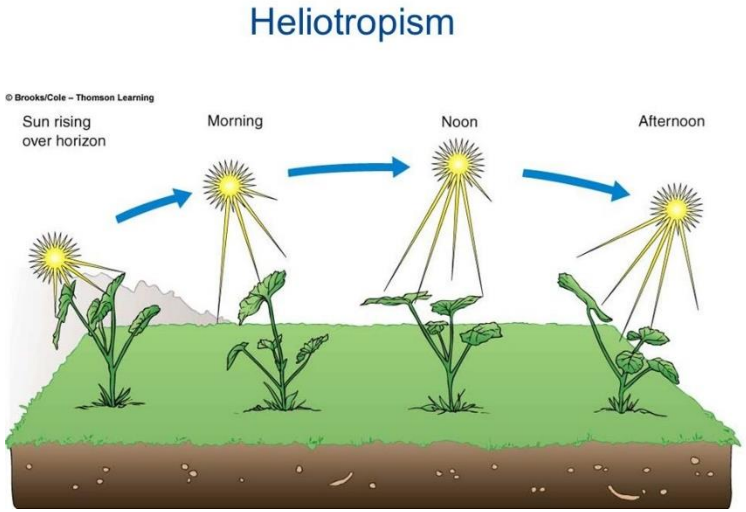


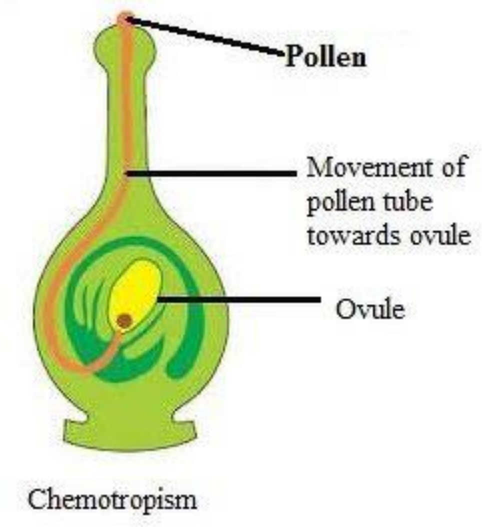
Movement

Tropism

Heliotropism refers to the diurnal or seasonal motion of plant parts (flowers or leaves) to move in response to the direction of the sun. For example, sunflower buds and leaves are heliotropic.

Chemotropism and **electrotropism** refer to movement or growth in response to chemicals and electric fields. Chemotropism plays an important role in plant reproduction, as the growth of pollen tube towards the ovule in the ovary (through the stigma and style) is due to positive chemotropism. The direction of growth of certain plant cells or organs can be modified by an applied electric field: for example maize roots curve towards a positive electric field.





Movement

Nastic Movement

Nastic movements are also growth or movement responses to stimuli, but differ from tropism in that with tropism the direction of the response depends on the direction of the stimulus, whereas with nastic movements the direction is independent of the stimulus's position.

For example, **photonasty** is the response of plants to a light stimulus- the opening of flowers in the daytime and their closure at night is a good example of photonastic movement. However, photonasty differs to phototropism because it occurs in response to the **intensity** of a light stimulus but not its direction.

Purple shamrock *Oxalis triangularis* exhibiting photonastic movement

View in slide mode to watch animation

Movement

Nastic Movement

Thigmonasty is the nastic response of a plant to touch or vibration. This is seen in many leguminous species of the Mimosoideae, for example *Mimosa pudica*, also called the sensitive plant, or 'touch me not'. This has compound leaves that droop suddenly when touched. Catclaw Brier, a prairie mimosa native to North America, also shuts its leaves on contact. The plant is eaten by herbivores, and this behaviour is thought to provide protection against grazing.

Other well-know examples of thigmonasty are seen in carnivorous plants such as the Venus Fly trap. When an insect lands on a trap formed by two curved lobes of a single leaf, a reflex is triggered causing the trap to switch rapidly from an open to a closed configuration.

View in slide mode to watch animation

Movement

Not all plant movements are in response to an environmental stimulus. Plants also have a widespread ability of autonomous, endogenous movement without apparent stimuli. **Circumnutations** are one type of such movement. This refers to the oscillatory movements of exploring stems and tendrils, and is especially seen in climbing plants seeking mechanical support.

Photoperiodism

In addition to growth and movement responses to light stimuli, plants can track the time of day and seasons to control key behaviours. This is known as **photoperiodism** and describes the developmental responses of plants to the relative lengths of light and dark periods. This is important in reproduction and phenological responses as it controls flowering. It is thought to be the result of interactions between a plant's "body clock" and light cues from its environment.

Many flowering plants detect seasonal changes in night length (or photoperiod) with photoreceptor proteins in order to signal when it is time to flower.

Some plants flower when the night length falls below a critical photoperiod threshold. These are long-day plants-examples include spinach and sugar beets. Others only flower when the night length exceeds a critical photoperiod: these are short-day plants. Examples include rice. Other species are day-neutral, where flowering does not depend on photoperiod.

In many plants, photoperiodism is controlled by the overlap between the day length cue and the plant's internal **circadian rhythms**.

Communication

Plants are in constant dialogue with other organisms in their environment. They communicate and interact with other plants, both aboveground and below, and they also communicate with other species, such as herbivores and mutualists. They emit cues that cause predictable reactions in other organisms and respond to such cues themselves.

Volatile Organic Compounds (VOCs) are one of the principle mechanisms plants use to communicate. These are chemical substances emitted in gaseous form that help plants to attract pollinators, defend against herbivore insects and parasites, and serve as signals to neighbouring **plants**.

Floral volatiles are emitted by floral tissue and give flowers their fragrance. Often made up of a blend of hundreds of compounds, they play a major role in pollinator attraction. Some flowers, such as petunias, also emit scents to deter herbivores.

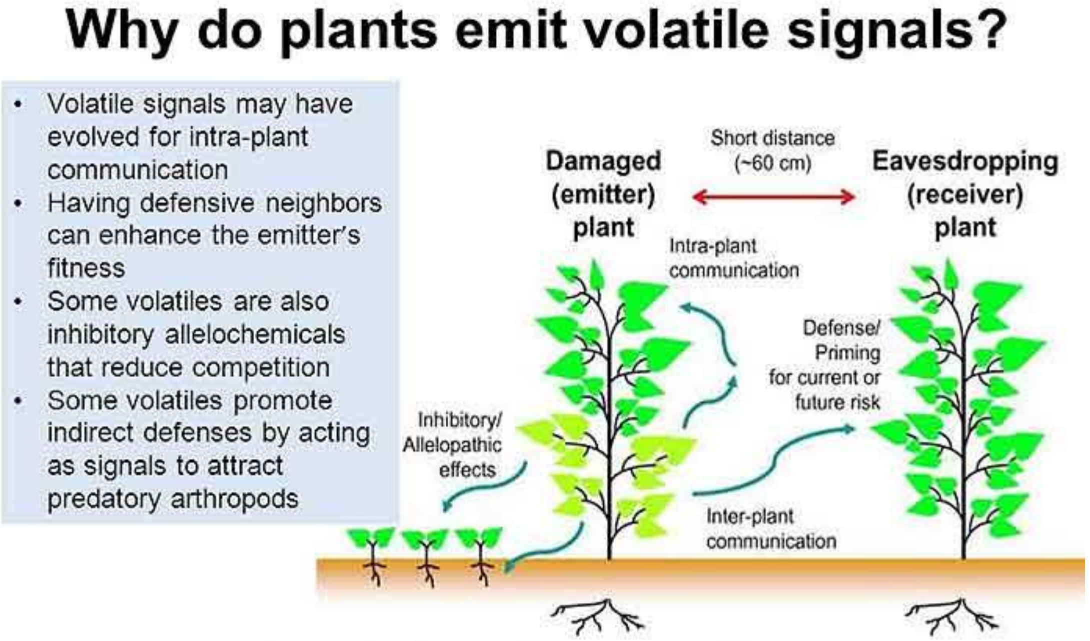
Herbivore-induced plant volatiles function as a defense response to herbivory. They serve as signals to attract natural enemies of herbivores such as parasitoids and predators. When insect predators chew leaves, plants respond by releasing VOCs into the air from the damaged plant tissues, advertising the presence of potential prey. For example, broad bean plants (*Vicia faba*) attacked by different species of aphid (*Acyrthosiphon pisum* and *A. fabae*) release different VOCs that attract different predators[1].

[1] Powell *et al*. 1998

Communication

VOC’s also play an important role in **plant−plant interactions**. When attacked by herbivorous arthropods, plants often emit a different blend of volatiles which initiate defense responses in neighbouring plants. This is a well-established response: many studies have shown that other plants detect these airborne signals and ramp up their production of chemical or other defense mechanisms in response.

For example, willow trees, poplars and sugar maples all warn each other about insect attacks: intact, undamaged trees near those that are infested emit insect-deterrent chemicals to ward off attack.



Why do plants emit volatile signals?

- Volatile signals may have evolved for intra-plant communication
- Having defensive neighbors can enhance the emitter’s fitness
- Some volatiles are also inhibitory allelochemicals that reduce competition
- Some volatiles promote indirect defenses by acting as signals to attract predatory arthropods

Communication

Plants also use VOCs to inhibit the growth of other plants. A good example comes from research into garlic mustard (*Alliaria petiolata*), which is native to Europe and Asia but invasive in North American forests.

Garlic mustard secretes benzyl isothiocyanate, a VOC which inhibits the growth of mycorrhizal fungi that support tree diversity. Changes in mycorrhizal fungal communities caused by the invasion of *A. petiolata* may influence tree seedling establishment[1].

Recent studies also suggest that other invasive plants, such as Canada goldenrod (*Solidago canadensis*), *Centaurea stoebe*, and narrow-leaf cattail (*Typha angustifolia*) produce chemicals that exert a detrimental physiological effect on native plants e.g. [2]

Invasive patch of *Alliaria petiolata*

1. Wolfe et al. (2008). The invasive plant *Alliaria petiolata* (garlic mustard) inhibits ectomycorrhizal fungi in its introduced range. Journal of Ecology, 96: 777-783
2. Yuan et al., (2012). Enhanced allelopathy and competitive ability of invasive plant Solidago canadensis in its introduced range. Journal of Plant Ecology, 6: 253–263

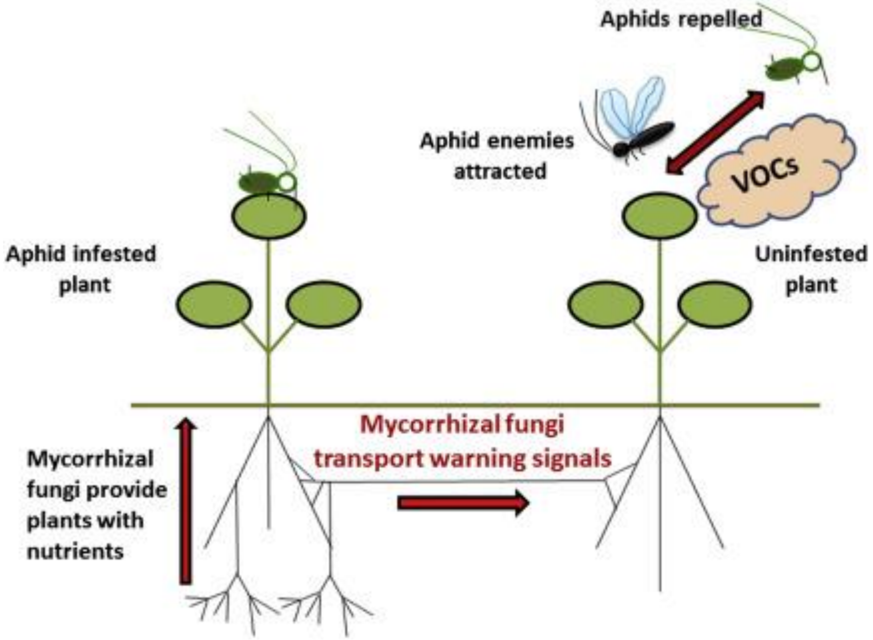
Communication

Below ground, plants 'talk' to each other through mycorrhizal networks, sensing chemicals through their roots.

Plants are able to monitor underground signals and react to the stresses their neighbours experience. Messages take the form of chemicals secreted by roots into the soil which are then detected through the roots of nearby plants.

What happens above ground influences what happens beneath the ground surface of a plant. When a plant’s leaves come into contact with another plant, it will allocate more resources to growing above ground than below

It has been experimentally shown that plants can change their growth strategy in response to the root signals from neighbouring plants. Plants exposed to the chemicals emitted by neighbouring plants that were touched responded by directing their resources into growing more leaves and fewer roots than control plants.



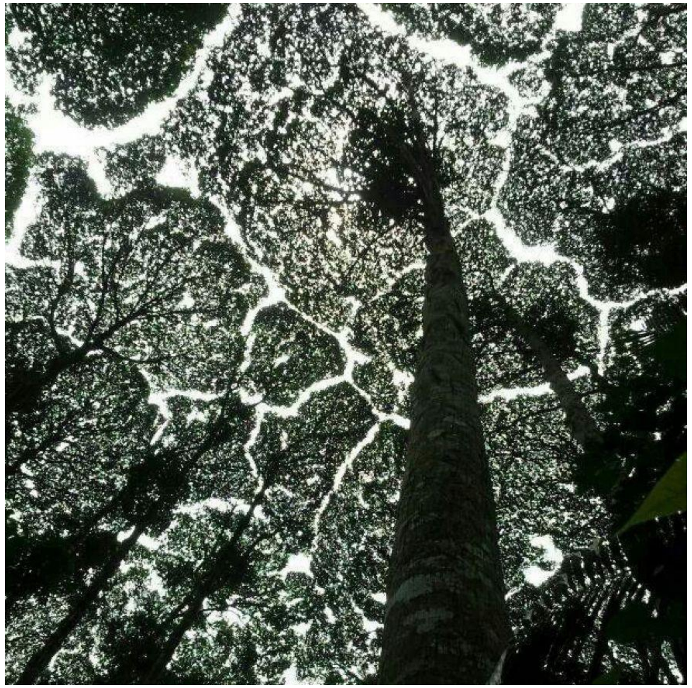
Communication

Crown shyness

Crown shyness, or intercrown spacing is a phenomenon observed in many tree species in which the crowns of mature trees do not touch each other. In so doing, the trees form a canopy that, when viewed from below, appear to create an intricate network of channels between the respective canopies.

Crown shyness is often seen within populations of the same species, but it can also occur between species or even within the same tree. Eucalyptus, Sitka spruce and Japanese larch are examples of species that exhibit crown shyness. The reasons it occurs are not definitely known, although different hypotheses have been proposed:

- It may prevent the spread of fungal or bacterial disease, or inhibit the spread of insects from one tree to the other.
- each tree forces its neighbours into a pattern that maximizes resource collection and minimizes harmful competition.
- Photosynthesis: the growing tips of trees use light levels to detect when another branch is near and stop growing when they’re too close.
- Reciprocal pruning: twigs and branches get broken when trees sway in the wind and hit one another. These collisions damage growth nodules, creating the gaps around each crown.
- It is a preventative measure that allows trees to minimize or avoid injury.



Discrimination and choice

Normally terms to describe behavioural aspects of intelligent organisms, it has been shown that plants have the ability to exhibit discrimination and choice. Higher plants do discriminate amongst many factors in their environment and choose to respond to those that are immediately relevant.

For example, the wetland grass species *Calamagrostis canadensis* grows by underground rhizomes. In experiments, a choice of habitats was provided in different compartments to young plants. The plants chose to grow in non-competitive, warmer and lighted conditions where they could forage more efficiently[1].

Given the choice between putting roots into soil containing competitors or unexploited soil, the garden pea *Pisum sativum* (garden pea) chose the latter[2].

In the tropics, lianas demonstrate the ability to discriminate, assess and make a decision. They do not attach themselves to trees unsuited for liana climbing - those with smooth trunks and umbrella tops- even when brought next to them.

1. MacDonald and Leiffers (1993). Rhizome plasticity and clonal foraging of Calamagrostis Canadensis en response to habitat heterogeneity. Journal of Ecology, 81: 769-776
2. Gersani et al. (1998). Density-dependent habitat selection in plants. Evolutionary Ecology, 12: 223-234

Kin recognition

Recent studies have shown that plants, too, have the ability to recognize other plants in their surroundings based on relatedness and identity. Plants even exhibit altruistic behaviour, giving their siblings a competitive edge in the wild[1].

Plants can recognize their kin through root systems and will compete more strongly for soil nutrients and water with non-sibling plants. When they recognize their kin, they grow differently in shape, taller, with more branches and fewer resources into leaves, therefore allowing their siblings to access precious sunlight

For example, kin recognition has been demonstrated in experiments with American searocket *Cakile edentula*, which produces more roots when grown in pots with strangers than when grown with kin plants (plants grown from seeds collected from the same mother plant)[2].

While plants prefer their kin, they crowd out competition when sharing a pot with strangers. Unrelated plants will not only compete underground for soil nutrients, but will attempt to push out the competition above ground in the ongoing struggle for light.

For example, the Yellow jewelweed *Impatiens pallida*, a common flowering plant, devotes less energy than usual to growing roots when surrounded by relatives. In the presence of genetically unrelated plants, individuals grow their roots as fast as they can[3].

1. Bias (2015). Shedding light on kin recognition response in plants. New Phytologist, 205: 4–6
2. Dudley and File (2007) Dudley SA, File AL. 2007. Kin recognition in an annual plant. Biology Letters 3: 435–438.
3. Murphy and Dudley (2009). Kin recognition: Competition and cooperation in *Impatiens* (Balsaminaceae). American Journal of Botany, 96: 1990-1996

Cognition

The idea of cognition in plants was first explored by Charles Darwin in the late 1800s, but only very recently has research into the mental capacites of plants really started to gain traction. This emerging field of study is known as **plant gnosophysiology** or plant perception.

Although controversial[1], recent research shows that plants are be capable of responding to and learning from stimuli in their surroundings in order to choose and make decisions that are most appropriate to ensure survival. In other words, they exhibit memory and alter their behaviours depending upon their previous experiences or the experiences of their parents.

Let us go back to *Mimosa pudica*, which as you remember, closes its leaves in a **thigmonastic** response to touch or sudden stress. Research has shown that when repeatedly exposed to a stressful situation that **doesn't** cause them harm, these plants learn and change their behaviour accordingly. When repeatedly exposed to drops of water on their leaves, the plants very quickly stopped curling in response, showing they had not only remembered, but learned that, in this scenario, leaf-closing was a waste of energy [2, however, see 3]

Other related research has shown that plants can "learn" via classical conditioning, similar to the famous Pavlov's dogs experiment. In experiments with Pea plants, they were conditioned by a fan to grow to towards a light source even when the light was not present. This is like Pavlov ringing the bell and the dogs salivating, even if there was no food around.

The mechanisms for this are not fully understood, but are thought to be based on a sophisticated, calcium-based signalling network in their cells similar to animals' memory process.

1. https://bigthink.com/robby-berman/getting-serious-about-plant-intelligence
2. Gagliano M et al (2014) Experience teaches plants to learn faster and forget slower in environments where it matters. Oecologia 175(1):63–72
3. Biegler (2017) Insufficient evidence for habituation in *Mimosa pudica*. Response to Gagliano et al. (2014). Oecologia 186: 33035

6.8

Resources

Suggested Reading

- Davies, N.B., Krebs, J.R. and West, S. A. (2012). An Introduction to Behavioural Ecology. 4th Edition. Wiley-Blackwell.
- Ward, A. and Webster, M. (2016). Sociality: The Behaviour of Group Living. Springer.
- Maynard Smith, J (1982). Evolution and the Theory of Games. Cambridge University Press.
- Clutton-Brock, T. (2016). Mammal Societies. John Wiley and Sons.
- Shuster, S.M. and Wade, M.J. (2003). Mating sytems and Strategies. Princeton University Press. https://www.researchgate.net/publication/291522031_Mating_Systems_and_Strategies
- Trewavas, A. 2014. Plant Behaviour and Intelligence. Oxford Scholarship Online
- Mancuso, S and Viola, A (2015). Brilliant Green: The Surprising History and Science of Plant Intelligence. Island Press.