Biological Interactions

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Chapter 1

Biological Interaction

Biological interactions are the interactions between organisms in a community. In the natural world no organism exists in absolute isolation, and thus every organism must interact with the environment and other organisms. An organism's interactions with its environment are fundamental to the survival of that organism and the functioning of the ecosystem as a whole.

The black walnut secretes a chemical from its roots that harms neighboring plants, an example of amensalism.

Primary Succession is a series of changes that occur in an area where no soil or organisms live. Secondary Succession is a series of changes occurring in an area where the ecosystems been disturbed, but soil and organisms are still existing.

In ecology, biological interactions are the relationships between two species in an ecosystem. These relationships can be categorized into many different classes of interactions based either on the effects or on the mechanism of the interaction. The interactions between two species vary greatly in these aspects as well as in duration and strength. Species may meet once in a generation (e.g. pollination) or live completely within another (e.g. endosymbiosis). Effects may range from one species eating the other (predation), to mutual benefit (mutualism). The interactions between two species need not be through direct contact. Due to the connected nature of ecosystems, species may affect each other through intermediaries such as shared resources or common enemies.

Interactions categorized by effect

Effect on X	Effect on Y	Type of interaction
0	0	Neutralism
-	0	Amensalism
+	0	Commensalism
-	-	Competition
+	+	Mutualism
+	-	Predation or Parasitism

Some types of relationships listed by the effect they have on each partner. '0' is no effect, '-' is detrimental, and '+' is beneficial.

Terms which explicitly indicate the quality of benefit or harm in terms of fitness experienced by participants in an interaction are listed below. There are six possible combinations, ranging from mutually beneficial through neutral to mutually harmful interactions. The level of benefit or harm is continuous and not discrete, such that an interaction may be trivially harmful through to deadly, for example. It is important to note that these interactions are not always static. In many cases, two species will interact differently under different conditions. This is particularly true in, but not limited to, cases where species have multiple, drastically different life stages.

Neutralism

Neutralism describes the relationship between two species which interact but do not affect each other. It describes interactions where the fitness of one species has absolutely no effect whatsoever on that of the other. True neutralism is extremely unlikely or even impossible to prove. When dealing with the complex networks of interactions presented by ecosystems, one cannot assert positively that there is absolutely no competition between or benefit to either species. Since true neutralism is rare or nonexistent, its usage is often extended to situations where interactions are merely insignificant or negligible.

Amensalism

Amensalism between two species involves one impeding or restricting the success of the other while the other species has no effect on it. It is a type of symbiosis. Usually this occurs when one organism exudes a chemical compound as part of its normal metabolism that is detrimental to another organism.

The bread mold Penicillium is a common example of this; penicillium secrete penicillin, a chemical that kills bacteria. A second example is the black walnut tree (*Juglans nigra*), which secrete juglone, a chemical that harms or kills some species of neighbouring plants, from its roots. This interaction may still increase the fitness of the non-harmed organism though, by removing competition and allowing it access to greater scarce resources. In this sense the impeding organism can be said to be negatively affected by the other's very existence, making it a +/- interaction. A third simple example is when sheep or cattle make trails in grass that they trample on, and without realizing, they are killing the grass.

Antibiosis or allelopathy also explain similar interactions.

It is the contrast of commensalism.

Competition

Competition is a mutually detrimental interaction between individuals, populations or species, but rarely between clades.

Synnecrosis is a particular case in which the interaction is so mutually detrimental that it results in death, as in the case of some parasitic relationships. It is a rare and necessarily short-lived condition as evolution selects against it. The term is seldom used.

Antagonism

This is not a bee, but a syrphid fly, a Batesian mimic.

In antagonistic interactions one species benefits at the expense of another. Predation is an interaction between organisms in which one organism captures biomass from another. It is often used as a synonym for carnivory but in its widest definition includes all forms of one organism eating another, regardless of trophic level (e.g. herbivory), closeness of association (e.g. parasitism and parasitoidism) and harm done to prey (e.g. grazing). Other interactions that cannot be classed as predation however are still possible, such as Batesian mimicry, where an organism bears a superficial similarity of at least one sort, such as a harmless plant coming to mimic a poisonous one. Intraguild predation occurs when an organism preys upon another of different species but at the same trophic level (e.g., coyotes kill and ingest gray foxes in southern California).

Ecological facilitation

The following two interactions can be classed as facilitative. *Facilitation* describes species interactions that benefit at least one of the participants and cause no harm to either. Facilitations can be categorized as mutualisms, in which both species benefit, or commensalisms, in which one species benefits and the other is unaffected. Much of classic ecological theory (e.g., natural selection, niche separation, metapopulation dynamics) has focused on negative interactions such as predation and competition, but positive interactions (facilitation) are receiving increasing focus in ecological research.

Commensalism

Commensalism benefits one organism and the other organism is neither benefited nor harmed. It occurs when one organism takes benefits by interacting with another organism by which the host organism is not affected. A good example is a remora living with a shark. Remoras eat leftover food from the shark. The shark is not affected in the process as remoras eat only leftover food of the shark which doesn't deplete the sharks resources.

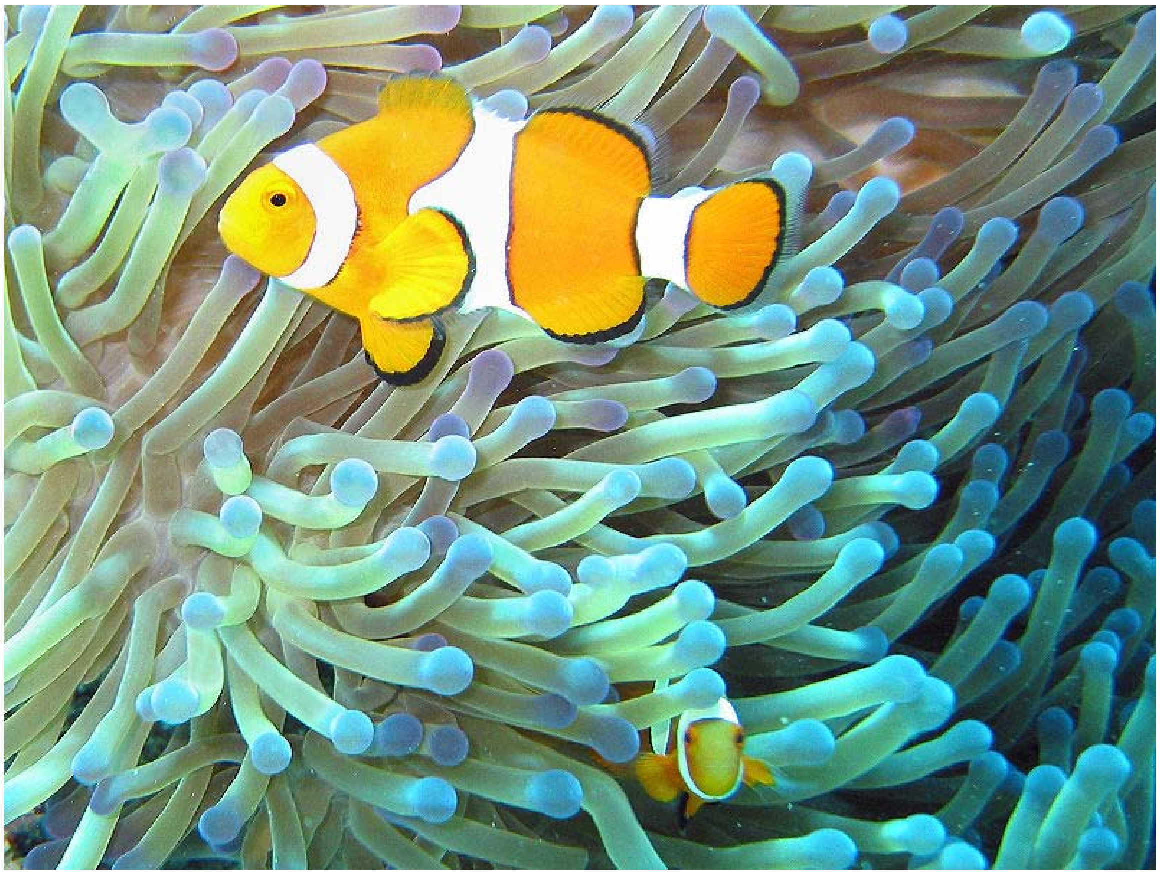
Mutualism

Pollination illustrates mutualism between flowering plants and their animal pollinators.

Mutualism is an interaction between two or more species, where species derive a mutual benefit, for example an increased carrying capacity. Similar interactions within a species are known as co-operation. Mutualism may be classified in terms of the closeness of association, the closest being symbiosis, which is often confused with mutualism. One or both species involved in the interaction may be obligate, meaning they cannot survive in the short or long term without the other species. Though mutualism has historically received less attention than other interactions such as predation, it is very important subject in ecology. Examples include cleaner fish, pollination and seed dispersal, gut flora and nitrogen fixation by fungi.

Interactions classified by mechanism

Symbiosis



Common Clownfish (*Amphiprion ocellaris*) in their Ritteri sea anemone (*Heteractis magnifica*) home. Both the fish and anemone benefit from this relationship, a case of mutualistic symbiosis.

The term symbiosis (Greek: living together) can be used to describe various degrees of close relationship between organisms of different species. Sometimes it is used only for cases where both organisms benefit, sometimes it is used more generally to describe all varieties of relatively tight relationships, i.e. even parasitism, but not predation. Some even go so far as to use it to describe predation.. It can be used to describe relationships where one organism lives on or in another, or it can be used to describe cases where organisms are related by mutual stereotypic behaviors.

In either case symbiosis is much more common in the living world and much more important than is generally assumed. Almost every organism has many internal parasites. A large percentage of herbivores have mutualistic gut fauna that help them digest plant matter, which is more difficult to digest than animal prey. Coral reefs are the result of mutalisms between coral organisms and various types of algae that live inside them. Most land plants and thus, one might say, the very existence of land ecosystems rely on mutualisms between the plants which fix carbon from the air, and Mycorrhyzal fungi which help in extracting minerals from the ground. The evolution of all eukaryotes (plants, animals, fungi, protists) is believed to have resulted from a symbiosis between various sorts of bacteria: endosymbiotic theory.

Competition

Male-male interference competition in red deer.

Competition can be defined as an interaction between organisms or species, in which the fitness of one is lowered by the presence of another. Limited supply of at least one resource (such as food, water, and territory) used by both is required. Competition is one of many interacting biotic and abiotic factors that affect community structure. Competition among members of the same species is known as intraspecific competition, while competition between individuals of different species is known as interspecific competition. Though intraspecific competition has been well documents the validity of interspecific competition, especially among large groups has been debated. Competition is not always a straightforward, direct interaction either, and can occur in both a direct and indirect fashion.

According to the competitive exclusion principle, species less suited to compete for resources should either adapt or die out. According to evolutionary theory, this competition within and between species for resources plays a critical role in natural selection.

Chapter 2

Competition (Biology)

Sea Anemones compete for the territory in tide pools

Competition is an interaction between organisms or species, in which the fitness of one is lowered by the presence of another. Limited supply of at least one resource (such as food, water, and territory) used by both is required. Competition both within and between species is an important topic in ecology, especially community ecology. Competition is one of many interacting biotic and abiotic factors that affect community structure. Competition among members of the same species is known as intraspecific competition, while competition between individuals of different species is known as interspecific competition. Competition is not always straightforward, and can occur in both a direct and indirect fashion..

According to the competitive exclusion principle, species less suited to compete for resources should either adapt or die out. According to evolutionary theory, this competition within and between species for resources plays a critical role in natural selection, however, competition may play less of a role than expansion among larger groups such as families..

Types of competition

By mechanism

The following terms describe mechanisms by which competition occurs, which can generally be divided into direct and indirect. These mechanisms apply equally to intraspecific and interspecific competition.

Male-male competition in red deer during rut is an example of interference competition within a species.

Interference competition

Occurs *directly* between individuals via aggression etc. when the individuals interfere with foraging, survival, reproduction of others, or by directly preventing their physical establishment in a portion of the habitat.

Exploitation competition

Occurs *indirectly* through a common limiting resource which acts as an intermediate. For example, use of resources depletes the amount available to others, or they compete for space. Also known as exploitative competition.

Apparent competition

Occurs *indirectly* between two species which are both preyed upon by the same predator. For example, species A and species B are both prey of predator C. The increase of species A will cause the decrease of species B because the increase of As would increase the number of predator Cs which in turn will hunt more of species B.

By species

Intraspecific competition

Intraspecific competition occurs when members of the same species vie for the same resources in an ecosystem. For example, two trees growing close together will compete for light above ground, and water and nutrients in the soil. Therefore, getting less resources, they will usually perform less well than if they grew by themselves. Although in this situation it may actually be more useful to think in terms of resource availability than competition. Adaptations to such an environment include growing taller, (where the specific prediction provided by the competition model is that all species in such a situation will grow as tall as possible). or developing a larger root system (where the specific prediction is that all species in the system will develop very deep root systems). The real question is whether these predictions are evidenced by our observations of the natural world.

Interspecific competition

Trees in this Bangladeshi forest are in interspecific competition for light.

Interspecific competition may occur when individuals of two separate species share a limiting resource in the same area. If the resource cannot support both populations, then lowered fecundity, growth, or survival may result in at least one species. Interspecific competition has the potential to alter populations, communities and the evolution of interacting species.

An example among animals could be the case of cheetahs and lions; since both species feed on similar prey, they are negatively impacted by the presence of the other because they will have less food, however they still persist together, despite the prediction that under competition one will displace the other. In fact, lions sometimes steal prey items killed by cheetahs. Potential competitors can also kill each other, and this phenomenon is called 'intraguild predation'. For example, in southern California coyotes often kill and eat gray foxes and bobcats, all three carnivores sharing the same stable prey (small mammals).

Competition has been observed between individuals, populations and species, but there is little evidence that competition has been the driving force in the evolution of large groups. For example, between reptiles and mammals. Mammals lived beside reptiles for many millions of years of time but were unable to gain a competitive edge until dinosaurs were devastated by the K-T Extinction.

Evolutionary strategies

In evolutionary contexts, competition is related to the concept of r/K selection theory, which relates to the selection of traits which promote success in particular environments. The theory originates from work on island biogeography by the ecologists Robert MacArthur and E. O. Wilson.

In r/K selection theory, selective pressures are hypothesised to drive evolution in one of two stereotyped directions: *r*- or *K*-selection. These terms, r and K, are derived from standard ecological algebra, as illustrated in the simple Verhulst equation of population dynamics:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

where *r* is the growth rate of the population (*N*), and *K* is the carrying capacity of its local environmental setting. Typically, r-selected species exploit empty niches, and produce many offspring, each of whom has a relatively low probability of surviving to adulthood. In contrast, K-selected species are strong competitors in crowded niches, and invest more heavily in much fewer offspring, each of whom has a relatively high probability of surviving to adulthood.

Chapter 3

Predation

Indian Python swallowing a full grown Chital deer at Mudumalai National Park

A juvenile Red-tailed Hawk eating a California Vole

Meat ants feeding on a cicada; some species can prey on individuals of far greater size, particularly when working cooperatively

In ecology, **predation** describes a biological interaction where a **predator** (an organism that is hunting) feeds on its **prey** (the organism that is attacked). Predators may or may not kill their prey prior to feeding on them, but the act of predation always results in the death of its prey and the eventual absorption of the prey's tissue through consumption. Other categories of consumption are herbivory (eating parts of plants) and detritivory, the consumption of dead organic material (detritus). All these consumption categories fall under the rubric of Consumer-Resource Systems It can often be difficult to separate our various types of feeding behaviors. For example, parasitic species prey on a host organism and then lay their eggs on it for their offspring to feed on it while it continues to live or on its decaying corpse after it has died. The key characteristic of predation however is the predator's direct impact on the prey population. On the other hand, detritivores simply eat dead organic material arising from the decay of dead individuals and have no direct impact on the "donor" organism(s).

Selective pressures imposed on one another has led to an evolutionary arms race between prey and predator, resulting in various antipredator adaptations.

The unifying theme in all classifications of predation is the predator lowering the fitness of its prey, or put another way, it reduces its prey's chances of survival, reproduction, or both. Ways of classifying predation surveyed here include grouping by trophic level or diet, by specialization, and by the nature of the predator's interaction with prey.

Functional classification

Classification of predators by the extent to which they feed on and interact with their prey is one way ecologists may wish to categorize the different types of predation. Instead of focusing on what they eat, this system classifies predators by the way in which they eat, and the general nature of the interaction between predator and prey species. Two factors are considered here: How close the predator and prey are physically (in the latter two cases the term *prey* may be replaced with *host*). Additionally, whether or not the prey are directly killed by the predator is considered, with true predation and parasitoidism involving certain death.

True predation

Lion and cub eating a Cape Buffalo

A true predator can commonly be known as one which kills and eats another organism. Whereas other types of predator all harm their prey in some way, this form certainly kills them. Predators may hunt actively for prey, or sit and wait for prey to approach within striking distance, as in ambush predators. Some predators kill large prey and dismember or chew it prior to eating it, such as a jaguar; others may eat their (usually much smaller) prey whole, as does a bottlenose dolphin swallowing a fish, or a snake or duck or stork swallowing a frog. Some predation entails venom which subdues a prey creature before the predator ingests the prey by killing, which the box jellyfish does, or disabling it, found in the behavior of the cone shell. In some cases the venom, as in rattlesnakes and some spiders, contributes to the digestion of the prey item even before the predator begins eating. In other cases, the prey organism may die in the mouth or digestive system of the predator. Baleen whales, for example, eat millions of microscopic plankton at once, the prey being broken down well after entering the whale. Seed predation and egg predation are other forms of true predation, as seeds and eggs represent potential organisms. Predators of this classification need not eat prey entirely, for example some predators cannot digest bones, while others can. Some may eat only part of an organism, as in grazing (see below), but still consistently cause its direct death.Some of the prominent examples of true predators are lion , tiger,etc.

Grazing

Grazing organisms may also kill their prey species, but this is seldom the case. While some herbivores like zooplankton live on unicellular phytoplankton and have no choice but to kill their prey, many only eat a small part of the plant. Grazing livestock may pull some grass out at the roots, but most is simply grazed upon, allowing the plant to regrow once again. Kelp is frequently grazed in subtidal kelp forests, but regrows at the base of the blade continuously to cope with browsing pressure. Animals may also be 'grazed' upon; female mosquitos land on hosts briefly to gain sufficient proteins for the development of their offspring. Starfish may be grazed on, being capable of regenerating lost arms.

Parasitism

Parasites can at times be difficult to distinguish from grazers. Their feeding behavior is similar in many ways, however they are noted for their close association with their host species. While a grazing species such as an elephant may travel many kilometers in a single day, grazing on many plants in the process, parasites form very close associations with their hosts, usually having only one or at most a few in their lifetime. This close living arrangement may be described by the term symbiosis, 'living together,' but unlike mutualism the association significantly reduces the fitness of the host. Parasitic organisms range from the macroscopic mistletoe, a parasitic plant, to microscopic internal parasites such as cholera. Some species however have more loose associations with their hosts. Lepidoptera (butterfly and moth) larvae may feed parasitically on only a single plant, or they may graze on several nearby plants. It is therefore wise to treat this classification system as a continuum rather than four isolated forms.

Parasitoidism

Parasitoids are organisms living in or on their host and feeding directly upon it, eventually leading to its death. They are much like parasites in their close symbiotic relationship with their host or hosts. Like the previous two classifications parasitoid predators do not kill their hosts instantly. However, unlike parasites, they are very similar to true predators in that the fate of their prey is quite inevitably death. A well known example of a parasitoids are the ichneumon wasps, solitary insects living a free life as an adult, then laying eggs on or in another species such as a caterpillar. Its larva(e) feed on the growing host causing it little harm at first, but soon devouring the internal organs until finally destroying the nervous system resulting in prey death. By this stage the young wasp(s) are developed sufficiently to move to the next stage in their life cycle. Though limited mainly to the insect order Hymenoptera, Diptera and Coleoptera parasitoids make up as much as 10% of all insect species.

Degree of specialization

An opportunistic Alligator swims with a deer.

Among predators there is a large degree of specialization. Many predators specialize in hunting only one species of prey. Others are more opportunistic and will kill and eat almost anything (examples: humans, leopards, and dogs). The specialists are usually particularly well suited to capturing their preferred prey. The prey in turn, are often equally suited to escape that predator. This is called an evolutionary arms race and tends to keep the populations of both species in equilibrium. Some predators specialize in certain classes of prey, not just single species. Almost all will switch to other prey (with varying degrees of success) when the preferred target is extremely scarce, and they may also resort to scavenging or a herbivorous diet if possible.

Trophic level

Mantis eating a bee.

Predators are often another organism's prey, and likewise prey are often predators. Though blue jays prey on insects, they may in turn be prey for cats and snakes, which, in the latter's case, may themselves be the prey of hawks. One way of classifying predators is by trophic level. Organisms which feed on autotrophs, the producers of the trophic pyramid, are known as herbivores or *primary consumers*; those that feed on heterotrophs such as animals are known as *secondary consumers*. Secondary consumers are a type of carnivore, but there are also tertiary consumers eating these carnivores, quartary consumers eating them, and so forth. Because only a fraction of energy is passed on to the next level, this hierarchy of predation must end somewhere, and very seldom goes higher than five or six levels, and may go only as high as three trophic levels (for example, a lion that preys upon large herbivores such as wildebeest which in turn eat grasses). A predator at the top of any food chain (that is, one that is preyed upon by no organism) is called an apex predator; examples include the orca, sperm whale, anaconda, Komodo dragon, tiger, lion, bald eagle, and Nile crocodile -- and even omnivorous humans and grizzly bears. An apex predator in one environment may not retain this position as a top predator if introduced to another habitat, such as a dog among alligators or a snapping turtle among jaguars; a predatory species introduced into an area where it faces no predators, such as a domestic cat or a dog in some insular environments, can become an apex predator by default.

Many organisms (of which humans are prime examples) eat from multiple levels of the food chain and thus make this classification problematic. A carnivore may eat both secondary and tertiary consumers, and its prey may itself be difficult to classify for similar reasons. Organisms showing both carnivory and herbivory are known as omnivores. Even herbivores such as the giant panda may supplement their diet with meat. Scavenging of carrion provides a significant part of the diet of some of the most fearsome predators. Carnivorous plants would be very difficult to fit into this classification, producing their own food but also digesting anything that they may trap. Organisms which eat detritivores or parasites would also be difficult to classify by such a scheme.

Predation as competition

An alternative view offered by Richard Dawkins is of predation as a form of competition: the genes of both the predator and prey are competing for the body (or 'survival machine') of the prey organism. This is best understood in the context of the gene centered view of evolution. Another manner in which predation and competition are connected is throughout intraguild predation. Intraguild predators are those that kill and eat other predators of different species at the same trophic level, and thus that are potential competitors.

Ecological role

Predators may increase the biodiversity of communities by preventing a single species from becoming dominant. Such predators are known as keystone species and may have a profound influence on the balance of organisms in a particular ecosystem. Introduction or removal of this predator, or changes in its population density, can have drastic cascading effects on the equilibrium of many other populations in the ecosystem. For example, grazers of a grassland may prevent a single dominant species from taking over.

The elimination of wolves from Yellowstone National Park had profound impacts on the trophic pyramid. Without predation, herbivores began to over-graze many woody brow species, affecting the area's plant populations. Additionally, wolves often kept animals from grazing in riparian areas, which protected beavers from having their food sources encroached upon. The removal of wolves had a direct effect on beaver populations, as their habitat became territory for grazing. Furthermore, predation keeps hydrological features such as creeks and streams in normal working order. Increased browsing on willows lenr and conifers along Blacktail Creek due to a lack of predation resulted in channel incision because those species helped slow the water down and hold the soil in place.

Adaptations and behavior

The act of predation can be broken down into a maximum of four stages: Detection of prey, attack, capture and finally consumption. The relationship between predator and prey is one which is typically beneficial to the predator, and detrimental to the prey species. Sometimes, however, predation has indirect benefits to the prey species, though the individuals preyed upon themselves do not benefit. This means that, at each applicable stage, predator and prey species are in an evolutionary arms race to maximize their respective abilities to obtain food or avoid being eaten. This interaction has resulted in a vast array of adaptations in both groups.

Camouflage of the dead leaf mantis makes it less visible to both its predators and prey.

One adaptation helping both predators and prey avoid detection is camouflage, a form of crypsis where species have an appearance which helps them blend into the background. Camouflage consists of not only color, but also shape and pattern. The background upon which the organism is seen can be both its environment (e.g. the praying mantis to the right resembling dead leaves) or other organisms (e.g. zebras' stripes blend in with each other in a herd, making it difficult for lions to focus on a single target). The more convincing camouflage is, the more likely it is that the organism will go unseen.

Mimicry in *Automeris io*.

Mimicry is a related phenomenon where an organism has a similar appearance to another species. One such example is the drone fly, which looks a lot like a bee, yet is completely harmless as it cannot sting at all. Another example of batesian mimicry is the io moth, (*Automeris io*), which has markings on its wings which resemble an owl's eyes. When an insectivorous predator disturbs the moth, it reveals its hind wings, temporarily startling the predator and giving it time to escape. Predators may also use mimicry to lure their prey, however. Female fireflies of the genus *Photuris*, for example, copy the light signals of other species, thereby attracting male fireflies which are then captured and eaten.

Predator

A South China Tiger as the predator feeding on the blesbuck, the prey.

Great blue heron with prey.

Lizard with prey.

While successful **predation** results in a gain of energy, hunting invariably involves energetic costs as well. When hunger is not an issue, most predators will generally not seek to attack prey since the costs outweight the benefits. For instance, a large predatory fish like a shark that is well fed in an aquarium will typically ignore the smaller fish swimming around it (while the prey fish take advantage of the fact that the apex predator is apparently uninterested). Surplus killing represents a deviation from this type of behaviour. The treatment of consumption in terms of cost-benefit analysis is known as optimal foraging theory, and has been quite successful in the study of animal behavior. Costs and benefits are generally considered in energy gain per unit time, though other factors are also important, such as essential nutrients that have no caloric value but are necessary for survival and health.

Social Predation offers the possibility of predators to kill creatures larger than those that members of the species could overpower singly. Lions, hyenas, wolves, dholes, African wild dogs, and piranhas can kill large herbivores that single animals of the same species could never dispatch. Social predation allows some animals to organize hunts of creatures that would easily escape a single predator; thus chimpanzees can prey upon colobus monkeys, and harris hawks can cut off all possible escapes for a doomed rabbit. Extreme specialization of roles is evident in some hunting that requires co-operation between predators of very different species: humans with the aid of falcons or dogs, or fishing with cormorants or dogs. Social predation is often very complex behavior, and not all social creatures (for example, domestic cats) perform it. Even without complex intelligence but instinct alone, some ant species can destroy much-larger creatures.

Size-selective predation involves predators preferring prey of a certain size. Large prey may prove troublesome for a predator, while small prey might prove hard to find and in any case provide less of a reward. This has led to a correlation between the size of predators and their prey. Size may also act as a refuge for large prey, for example adult elephants are generally safe from predation by lions, but juveniles are vulnerable.

It has been observed that well-fed predator animals in a lax captivity (for instance, pet or farm animals) will usually differentiate between putative prey animals who are familiar co-inhabitants in the same human area from wild ones outside the area. This interaction can range from peaceful coexistence to close companionship; motivation to ignore the predatory instinct may result from mutual advantage or fear of reprisal from human masters who have made clear that harming co-inhabitants will not be tolerated. Pet cats and pet mice, for example, may live together in the same human residence without incident as companions. Pet cats and pet dogs under human mastership often depend on each other for warmth, companionship, and even protection, particularly in rural areas.

Antipredator adaptations

Antipredator adaptations have evolved in prey populations due to the selective pressures of predation over long periods of time.

Aggression

Predatory animals often use their usual methods of attacking prey to inflict or to threaten grievous injury to their own predators. The electric eel uses the same electrical current to kill prey and to defend itself against animals (anacondas, caimans, jaguars, egrets, cougars, giant otters, humans, and dogs) that ordinarily prey upon fish similar to an electric eel in size; the electric eel thus remains an apex predator in a predator-rich environment. Many non-predatory prey animals, such as a zebra, can give a strong kick that can maim or kill, while others charge with tusks or horns.

Mobbing behavior

Mobbing behavior occurs when members of a species drive away their predator by cooperatively attacking or harassing it. Most frequently seen in birds, mobbing is also seen in other social animals. For example, nesting gull colonies are widely seen to attack intruders, including humans. Costs of mobbing behavior include the risk of engaging with predators, as well as energy expended in the process, but it can aid the survival of members of a species.

While mobbing has evolved independently in many species, it tends to be present only in those whose young are frequently preyed on, especially birds. It may complement cryptic behavior in the offspring themselves, such as camouflage and hiding. Mobbing calls may be made prior to or during engagement in harassment.

Mobbing can be an interspecies activity: it is common for birds to respond to mobbing calls of a different species. Many birds will show up at the sight of mobbing and watch and call, but not participate. It should also be noted that some species can be on both ends of a mobbing attack. Crows are frequently mobbed by smaller songbirds as they prey on eggs and young from these birds' nests, but these same crows will cooperate with smaller birds to drive away hawks or larger mammalian predators. On occasion, birds will mob animals that pose no threat.

Advertising unprofitability

Thomson's Gazelles exhibit stotting behavior.

A Thomson's Gazelle seeing a predator approach may start to run away, but then slow down and *stot*. Stotting is jumping into the air with the legs straight and stiff, and the white rear fully visible. Stotting is maladaptive for outrunning predators; evidence suggests that stotting signals an unprofitable chase. For example, cheetahs abandon more hunts when the gazelle stots, and in the event they do give chase, they are far less likely to make a kill.

Aposematism, where organisms are brightly colored as a warning to predators, is the antithesis of camouflage. Some organisms pose a threat to their predators—for example they may be poisonous, or able to harm them physically. Aposematic coloring involves bright, easily recognizable and unique colors and patterns. Upon being harmed (e.g. stung) by their prey, the appearance in such an organism will be remembered as something to avoid.

Chemical defense

Some organisms have evolved chemical weapons which are effective deterrents against predation. It is most common in insects, but the skunk is a particularly dramatic mammalian example. Other examples include the Bombardier beetle which can accurately shoot a predator with a stream of boiling poison, the Ornate moth which excretes a frothy alkaloid mixture, and the Pacific beetle cockroach sprays a quinone mixture from modified spiracles.

Terrain Fear Factor

The "terrain fear factor" is an idea which assesses the risks associated with predator/prey encounters. This idea suggests that prey will change their usual habits to adjust to the terrain and its effect on the species' predation. For example, a species may forage in a terrain with a lower predation risk as opposed to one with high predation risk.

Population dynamics

It is fairly clear that predators tend to lower the survival and fecundity of their prey, but on a higher level of organization, populations of predator and prey species also interact. It is obvious that predators depend on prey for survival, and this is reflected in predator populations being affected by changes in prey populations. It is not so obvious, however, that predators affect prey populations. Eating a prey organism may simply make room for another if the prey population is approaching its carrying capacity.

The population dynamics of predator-prey interactions can be modelled using the Lotka–Volterra equations. These provide a mathematical model for the cycling of predator and prey populations.

Predators tend to select young, weak, and ill individuals.

Evolution of predation

Predation appears to have become a major selection pressure shortly before the Cambrian period—around 550 million years ago—as evidenced by the almost simultaneous development of calcification in animals and algae, and predation-avoiding burrowing. However, predators had been grazing on micro-organisms since at least 1,000 million years ago.

Humans and predation

As predators

Humans are omnivorous and use tools to exploit their environments; from snares, clubs, spears, fishing gear, firearms to boats and motor vehicles. Humans even use other predatory species, (such as dogs, cormorants, and falcons) in hunting and fishing; some people even enlist such non-predatory beasts, like horses, camels, and elephants in getting approaches to prey.

Humans have reshaped huge expanses of the world as ranges and farms for the raising of livestock, poultry, and fish to be eaten as meat. However, it can be debated whether or not harvesting livestock fits strictly in the definition of predation.

Human raising and eating of livestock is part of agriculture, and involves the feeding of and caring for animals, followed by their being slaughtered with an appropriate tool, cutting up, and cooking. In many cultures, animals are hunted or farmed by specialists (such as ranchers or fishermen), brought to a marketplace, and sold in pieces to the people who actually consume the meat.

As prey

A lone naked human is at a physical disadvantage to other comparable apex predators in areas such as speed, bone density, weight, and physical strength. Humans also lack innate weaponry such as claws. Without crafted weapons, society, or cleverness, a lone human can easily be defeated by fit predatory animals, such as wild dogs, big cats and bears. There are even recorded instances of lone humans being preyed upon by large carnivores. However humans are not solitary creatures; they are social animals with highly developed social behaviors. Further humans and their ancestors (such as *Homo erectus*) have been using stone tools and weapons for well over a million years. Anatomically modern humans have been apex predators since they first evolved, and many species of carnivorous megafauna actively avoid interacting with humans; the primary environmental competitor for a human is other humans. Cannibalism has occurred in various places, among various cultures, and for various reasons. At least a few people, such as the Donner party, are said to have resorted to it in desperation.

In conservation

Predators are an important consideration in matters relating to conservation. Introduced predators may prove too much for populations which have not coevolved with them, leading to possible extinction. This will depend largely on how well the prey species can adapt to the new species, and or not the predator can turn to alternative food sources when prey populations fall to minimal levels. If a predator can use an alternative prey instead, it may shift its diet towards that species, while still eating the last remaining prey organisms. On the other hand the prey species may be able to survive if the predator has no alternative prey—in this case its population will necessarily crash following the decline in prey, allowing some small proportion of prey to survive. Introduction of an alternative prey may well lead to the extinction of prey, as this constraint is removed.

Predators are often the species endangered themselves, especially apex predators who are often in competition with humans. Competition for prey from other species could prove the end of a predator—if their ecological niche overlaps completely with that of another the competitive exclusion principle requires only one can survive. Loss of prey species may lead to coextinction of their predator. In addition, because predators are found in higher trophic levels, they are less abundant and much more vulnerable to extinction.

Biological pest control

Predators may be put to use in conservation efforts to control introduced species. Although the aim in this situation is to remove the introduced species entirely, keeping its abundance down is often the only possibility. Predators from its natural range may be introduced to control populations, though in some cases this has little effect, and may even cause unforeseen problems. Besides their use in conservation biology, predators are also important for controlling pests in agriculture. Natural predators are an environmentally friendly and sustainable way of reducing damage to crops, and are one alternative to the use of chemical agents such as pesticides.

Chapter 4

Ecological Facilitation

Facilitation describes species interactions that benefit at least one of the participants and cause harm to neither. Facilitations can be categorized as mutualisms, in which both species benefit, or commensalisms, in which one species benefits and the other is unaffected. Much of classic ecological theory (*e.g.*, natural selection, niche separation, metapopulation dynamics) has focused on negative interactions such as predation and competition, but positive interactions (facilitation) are receiving increasing focus in ecological research. Here we, addresses both the mechanisms of facilitation and the increasing information available concerning the impacts of facilitation on community ecology.

Categories

Nurse log harboring a western hemlock tree

There are two basic categories of facilitative interactions:

- A *mutualism* is an interaction between species that is beneficial to both. A familiar example of a mutualism is the relationship between flowering plants and their pollinators. The plant benefits from the spread of pollen between flowers, while the pollinator receives some form of nourishment, either from nectar or the pollen itself.
- A *commensalism* is an interaction in which one species benefits and the other species is unaffected. Epiphytes (plants growing on other plants, usually trees) have a commensal relationship with their host plant because the epiphyte benefits in some way (*e.g.*, by escaping competition with terrestrial plants or by gaining greater access to sunlight) while the host plant is apparently unaffected.

Strict categorization, however, is not possible for some complex species interactions. For example, seed germination and survival in harsh environments is often higher under so-called nurse plants than on open ground. A nurse plant is one with an established canopy, beneath which germination and survival are more likely due to increased shade, soil moisture, and nutrients. Thus, the relationship between seedlings and their nurse plants is commensal. However, as the seedlings grow into established plants, they are likely to compete with their former benefactors for resources.

Mechanisms

The beneficial effects of species on one another are realized in various ways, including refuge from physical stress, predation, and competition, improved resource availability, and transport.

Refuge from physical stress

Facilitation may act by reducing the negative impacts of a stressful environment. As described above, nurse plants facilitate seed germination and survival by alleviating stressful environmental conditions. A similar interaction occurs between the red alga *Chondrus crispus* and the canopy-forming seaweed *Fucus* in intertidal sites of southern New England, USA. The alga survives higher in the intertidal zone—where temperature and desiccation stresses are greater—only when the seaweed is present because the canopy of the seaweed offers protection from those stresses. The previous examples describe facilitation of individuals or of single species, but there are also instances of a single facilitator species mediating some community-wide stress, such as disturbance. An example of such "whole-community" facilitation is substrate stabilization of cobble beach plant communities in Rhode Island, USA, by smooth cordgrass (*Spartina alterniflora*). Large beds of cordgrass buffer wave action, thus allowing the establishment and persistence of a community of less disturbance-tolerant annual and perennial plants below the high-water mark.

In general, facilitation is more likely to occur in physically stressful environments than in favorable environments, where competition may be the most important interaction among species. This can also occur in a single habitat containing a gradient from low to high stress. For example, along a New England, USA, salt marsh tidal gradient, a presence of black needle rush (*Juncus gerardi*) increased the fitness of marsh elder (*Iva*) shrubs in lower elevations, where soil salinity was higher. The rush shaded the soil, which decreased evapotranspiration, and in turn decreased soil salinity. However, at higher elevations where soil salinity was lower, marsh elder fitness was decreased in the presence of the rush, due to increased competition for resources. Thus, the nature of species interactions may shift with environmental conditions.

Refuge from predation

'Bubbles' of honeydew on aphids.

Another mechanism of facilitation is a reduced risk of being eaten. Nurse plants, for example, not only reduce abiotic stress, but may also physically impede herbivory of seedlings growing under them. In both terrestrial and marine environments, herbivory of palatable species is reduced when they occur with unpalatable species. These "associational refuges" may occur when unpalatable species physically shield the palatable species, or when herbivores are "confused" by the inhibitory cues of the unpalatable species. Herbivory can also reduce predation of the herbivore, as in the case of the red-ridged clinging crab (*Mithrax forceps*) along the North Carolina, USA, coastline. This crab species takes refuge in the branches of the compact Ivory Bush Coral (*Oculina arbuscula*) and feeds on seaweed in the vicinity of the coral. The reduced competition with seaweed enhances coral growth, which in turn provides more refuge for the crab. A similar case is that of the interaction between swollen-thorn acacia trees (*Acacia* spp.) and certain ants (*Pseudomyrmex* spp.) in Central America. The acacia provides nourishment and protection (inside hollow thorns) to the ant in return for defense against herbivores. In contrast, a different type of facilitation between ants and sap-feeding insects may increase plant predation. By consuming sap, plant pests such as aphids produce a sugar-rich waste product called honeydew, which is consumed by ants in exchange for protection of the sap-feeders against predation.

Refuge from competition

Another potential benefit of facilitation is insulation from competitive interactions. Like the now familiar example of nurse plants in harsh environments, *nurse logs* in a forest are sites of increased seed germination and seedling survival because the raised substrate of a log frees seedlings from competition with plants and mosses on the forest floor. The crab-coral interaction described above is also an example of refuge from competition, since the herbivory of crabs on seaweed reduces competition between coral and seaweed. Similarly, herbivory by sea urchins (*Strongylocentrotus droebachiensis*) on kelps (*Laminaria* spp.) can protect mussels (*Modiolus modiolus*) from overgrowth by kelps competing for space in the subtidal zone of the Gulf of Maine, USA.

Improved resource availability

Facilitation can increase access to limiting resources such as light, water, and nutrients for interacting species. For example, epiphytic plants often receive more direct sunlight in the canopies of their host plants than they would on the ground. Also, nurse plants increase the amount of water available to seedlings in dry habitats because of reduced evapotranspiration beneath the shade of nurse plant canopies. However, the most familiar examples of increased access to resources through facilitation are the mutualistic transfers of nutrients between symbiotic organisms. A symbiosis is a prolonged, close association between organisms, and some examples of mutualistic symbioses include:

Gut flora
: Associations between a host species and a microbe living in the host's digestive tract, wherein the host provides habitat and nourishment to the microbe in exchange for digestive services. For example, termites receive nourishment from cellulose digested by microbes inhabiting their gut.

Lichens
: Associations between fungi and algae, wherein the fungus receives nutrients from the alga, and the alga is protected from harsh conditions causing desiccation.

Corals
: Associations between reef-building corals and photosynthetic algae called zooxanthellae, wherein the zooxanthellae provide nutrition to the corals in the form of photosynthate, in exchange for nitrogen in coral waste products.

Mycorrhizae
: Associations between fungi and plant roots, wherein the fungus facilitates nutrient uptake (particularly nitrogen) by the plant in exchange for carbon in the form of sugars from the plant root. There is a parallel example in marine environments of sponges on the roots of mangroves, with a relationship analogous to that of mycorrhizae and terrestrial plants.

Transport

The movement by animals of items involved in plant reproduction is usually a mutualistic association. Pollinators may increase plant reproductive success by reducing pollen waste, increasing dispersal of pollen, and increasing the probability of sexual reproduction at low population density. In return, the pollinator receives nourishment in the form of nectar or pollen. Animals may also disperse the seed or fruit of plants, either by eating it (in which case they receive the benefit of nourishment) or by passive transport, such as seeds sticking to fur or feathers.

Community Effects

Although facilitation is often studied at the level of individual species interactions, the effects of facilitation are often observable at the scale of the community, including impacts to spatial structure, diversity, and invasibility.

Spatial structure

Many facilitative interactions directly affect the distribution of species. As discussed above, transport of plant propagules by animal dispersers can increase colonization rates of more distant sites, which may impact the distribution and population dynamics of the plant species. Facilitation most often affects distribution by simply making it possible for a species to occur in a site where some environmental stress would otherwise prohibit growth of that species. This is apparent in whole-community facilitation by a foundation species, such as sediment stabilization in cobble beach plant communities by smooth cordgrass. A facilitating species may also help drive the progression from one ecosystem type to another, as mesquite apparently does in the grasslands of the Rio Grande Plains. As a nitrogen-fixing tree, mesquite establishes more readily than other species on nutrient-poor soils, and following establishment, mesquite acts as a nurse plant for seedlings of other species. Thus, mesquite facilitates the dynamic spatial shift from grassland to savanna to woodland across the habitat.

Diversity

Facilitation affects community diversity (defined in this context as the number of species in the community) by altering competitive interactions. For example, intertidal mussels increase total community species diversity by displacing competitive large sessile species such as seaweed and barnacles. Although the mussels decrease diversity of primary space holders (i.e., large sessile species), a larger number of invertebrate species are associated with mussel beds than with other primary space holders, so total species diversity is higher when mussels are present. The effect of facilitation on diversity could also be reversed, if the facilitation creates a competitive dominance that excludes more species than it permits.

Invasibility

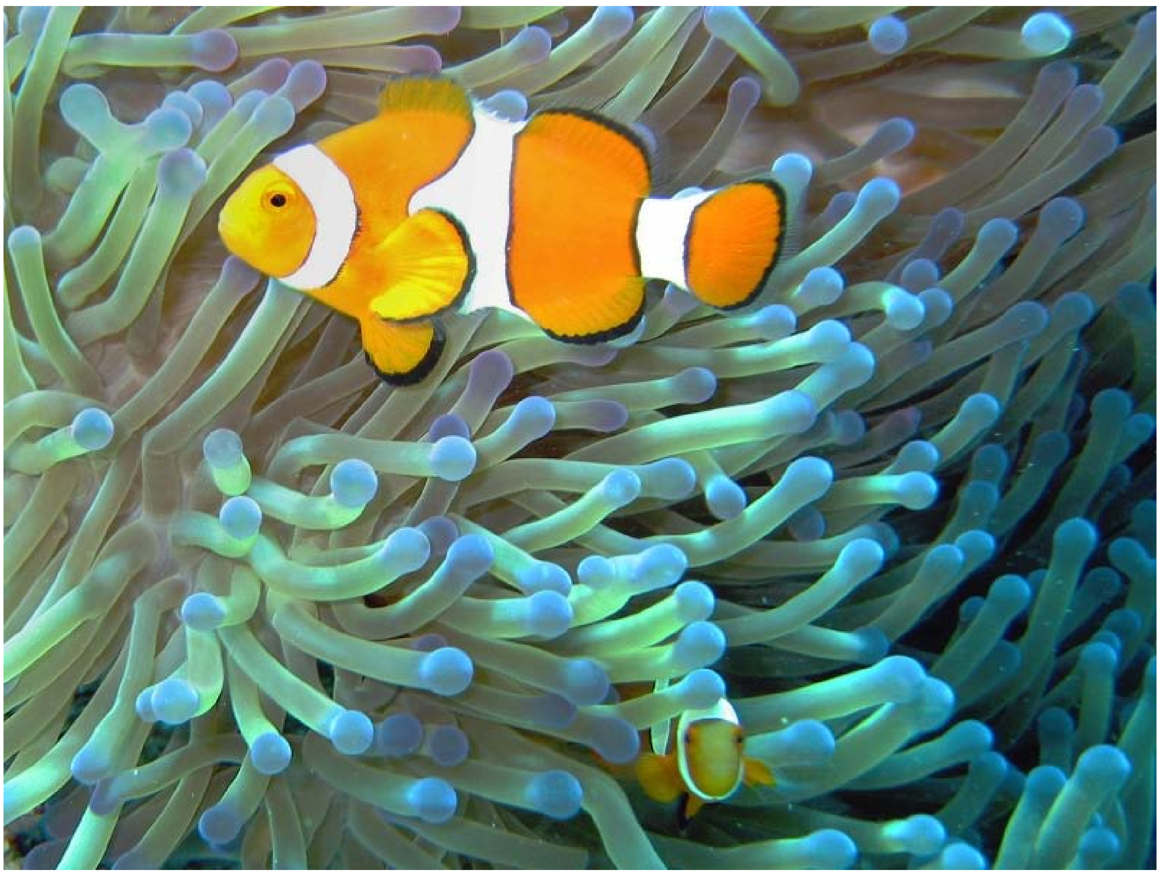
Facilitation of non-native species, either by native species or other non-native species, may increase the invasibility of a community, or the ease with which non-native species become established in a community. In an examination of 254 published studies of introduced species, 22 of 190 interactions studied between introduced species in the studies were facilitative. It is worth noting that 128 of the 190 examined interactions were predator-prey relationships of a single plant-eating insect reported in a single study, which may have overemphasized the importance of negative interactions. Introduced plants are also facilitated by native pollinators, dispersers, and mycorrhizae. Thus, positive interactions must be considered in any attempt to understand the invasibility of a community.

Conclusion

Facilitation is a significant ecological process that produces community-level effects through individual interactions. By improving dispersal, increasing access to resources, and providing protection from stress, predation, and competition, facilitation can impact community structure, diversity, and invasibility. Incorporation of facilitation into such classic theories as natural selection and niche separation should be a goal of current and future ecologists. This will require further research into the mechanisms of facilitation at the level of individuals, and the impacts of facilitation at the level of population, community, and ecosystem. Continued study of positive species interactions will serve to improve our understanding of processes and application of theories.

Chapter 5

Symbiosis



In a symbiotic mutualism, the clownfish feeds on small invertebrates which otherwise potentially could harm the sea anemone, and the fecal matter from the clownfish provides nutrients to the sea anemone. The clownfish is additionally protected from predators by the anemone's stinging cells, to which the clownfish is immune.

Symbiosis is close and often long-term interactions between different biological species. In 1877 Bennett used the word symbiosis (which previously had been used of people living together in community) to describe the mutualistic relationship in lichens. In 1879 by the German mycologist Heinrich Anton de Bary, defined it as "the living together of unlike organisms."

The definition of symbiosis is in flux, and the term has been applied to a wide range of biological interactions. The symbiotic relationship may be categorized as mutualistic, commensal, or parasitic in nature.

Some symbiotic relationships are obligate, meaning that both symbionts entirely depend on each other for survival. For example, many lichens consist of fungal and photosynthetic symbionts that cannot live on their own. Others are facultative, meaning that they can but do not have to live with the other organism.

Symbiotic relationships include those associations in which one organism lives on another (ectosymbiosis, such as mistletoe), or where one partner lives inside the other (endosymbiosis, such as lactobacilli and other bacteria in humans or zooxanthelles in corals).

Physical interaction

Alder tree root nodule

Endosymbiosis is any symbiotic relationship in which one symbiont lives within the tissues of the other, either in the intracellular space or extracellularly. Examples are rhizobia, nitrogen-fixing bacteria that live in root nodules on legume roots; actinomycete nitrogen-fixing bacteria called *Frankia*, which live in alder tree root nodules; single-celled algae inside reef-building corals; and bacterial endosymbionts that provide essential nutrients to about 10%–15% of insects.

Ectosymbiosis, also referred to as *exosymbiosis*, is any symbiotic relationship in which the symbiont lives on the body surface of the host, including the inner surface of the digestive tract or the ducts of exocrine glands. Examples of this include ectoparasites such as lice, commensal ectosymbionts such as the barnacles that attach themselves to the jaw of baleen whales, and mutualist ectosymbionts such as cleaner fish.

Mutualism

Hermit crab, *Calcinus laevimanus*, with sea anemone.

Mutualism is any relationship between individuals of different species where both individuals derive a benefit. Generally, only lifelong interactions involving close physical and biochemical contact can properly be considered symbiotic. Mutualistic relationships may be either obligate for both species, obligate for one but facultative for the other, or facultative for both. Many biologists restrict the definition of symbiosis to close mutualist relationships.

A large percentage of herbivores have mutualistic gut fauna that help them digest plant matter, which is more difficult to digest than animal prey. Coral reefs are the result of mutualisms between coral organisms and various types of algae that live inside them. Most land plants and land ecosystems rely on mutualisms between the plants, which fix carbon from the air, and mycorrhyzal fungi, which help in extracting minerals from the ground.

An example of mutual symbiosis is the relationship between the ocellaris clownfish that dwell among the tentacles of Ritteri sea anemones. The territorial fish protects the anemone from anemone-eating fish, and in turn the stinging tentacles of the anemone protect the clownfish from its predators. A special mucus on the clownfish protects it from the stinging tentacles.

Another example is the goby fish, which sometimes lives together with a shrimp. The shrimp digs and cleans up a burrow in the sand in which both the shrimp and the goby fish live. The shrimp is almost blind, leaving it vulnerable to predators when above ground. In case of danger the goby fish touches the shrimp with its tail to warn it. When that happens both the shrimp and goby fish quickly retract into the burrow.

One of the most spectacular examples of obligate mutualism is between the siboglinid tube worms and symbiotic bacteria that live at hydrothermal vents and cold seeps. The worm has no digestive tract and is wholly reliant on its internal symbionts for nutrition. The bacteria oxidize either hydrogen sulfide or methane which the host supplies to them. These worms were discovered in the late 1980s at the hydrothermal vents near the Galapagos Islands and have since been found at deep-sea hydrothermal vents and cold seeps in all of the world's oceans.

There are also many types of tropical and sub-tropical ants that have evolved very complex relationships with certain tree species.

Commensalism

Phoretic mites on a fly (*Pseudolynchia canariensis*).

Commensalism describes a relationship between two living organisms where one benefits and the other is not significantly harmed or helped. It is derived from the English word commensal used of human social interaction. The word derives from the medieval Latin word, formed from *com*- and *mensa*, meaning "sharing a table".

Commensal relationships may involve one organism using another for transportation (phoresy) or for housing (inquilinism), or it may also involve one organism using something another created, after its death (metabiosis). Examples of metabiosis are hermit crabs using gastropod shells to protect their bodies and spiders building their webs on plants.

Parasitism

Flea bites on a human is an example of parasitism (the flea as parasite to the human host in this case).

A parasitic relationship is one in which one member of the association benefits while the other is harmed. Parasitic symbioses take many forms, from endoparasites that live within the host's body to ectoparasites that live on its surface. In addition, parasites may be necrotrophic, which is to say they kill their host, or biotrophic, meaning they rely on their host's surviving. Biotrophic parasitism is an extremely successful mode of life. Depending on the definition used, as many as half of all animals have at least one parasitic phase in their life cycles, and it is also frequent in plants and fungi. Moreover, almost all free-living animals are host to one or more parasite taxa. An example of a biotrophic relationship would be a tick feeding on the blood of its host.

Amensalism

Amensalism is the type of symbiotic relationship that exists where one species is inhibited or completely obliterated and one is unaffected. This type of symbiosis is relatively uncommon in rudimentary reference texts, but is omnipresent in the natural world. An example is a sapling growing under the shadow of a mature tree. The mature tree can begin to rob the sapling of necessary sunlight and, if the mature tree is very large, it can take up rainwater and deplete soil nutrients. Throughout the process the mature tree is unaffected. Indeed, if the sapling dies, the mature tree gains nutrients from the decaying sapling. Note that these nutrients become available because of the sapling's decomposition, rather than from the living sapling, which would be a case of parasitism.

Symbiosis and evolution

Leafhoppers protected by an army of meat ants

While historically, symbiosis has received less attention than other interactions such as predation or competition, it is increasingly recognised as an important selective force behind evolution, with many species having a long history of interdependent co-evolution. In fact, the evolution of all eukaryotes (plants, animals, fungi, and protists) is believed under the endosymbiotic theory to have resulted from a symbiosis between various sorts of bacteria.

Vascular Plants

Up to 80% of vascular plants worldwide form symbiotic relationships with fungi, for example, in arbuscular mycorrhiza.

Symbiogenesis

The biologist Lynn Margulis, famous for her work on endosymbiosis, contends that symbiosis is a major driving force behind evolution. She considers Darwin's notion of evolution, driven by competition, as incomplete and claims that evolution is strongly based on co-operation, interaction, and mutual dependence among organisms. According to Margulis and Dorion Sagan, "Life did not take over the globe by combat, but by networking."

Co-evolution

Symbiosis played a major role in the co-evolution of flowering plants and the animals that pollinate them. Many plants that are pollinated by insects, bats, or birds have highly specialized flowers modified to promote pollination by a specific pollinator that is also correspondingly adapted. The first flowering plants in the fossil record had relatively simple flowers. Adaptive speciation quickly gave rise to many diverse groups of plants, and, at the same time, corresponding speciation occurred in certain insect groups. Some groups of plants developed nectar and large sticky pollen, while insects evolved more specialized morphologies to access and collect these rich food sources. In some taxa of plants and insects the relationship has become dependent, where the plant species can only be pollinated by one species of insect.

Chapter 6

Camouflage

A flounder blending in with the gravel on the sea floor.

A camouflaged sniper, an example of military camouflage

Camouflage is a method of crypsis (hiding). It allows an otherwise visible organism or object to remain unnoticed, by blending with its environment. Examples include a tiger's stripes, the battledress of a modern soldier and a butterfly camouflaging itself as a leaf. The theory of camouflage covers the various strategies which are used to achieve this effect.

In nature

Cryptic coloration is the most common form of camouflage, found to some extent in the majority of species. The simplest way is for an animal to be of a color similar to its surroundings. Examples include the "earth tones" of deer, squirrels, or moles (to match trees or dirt), or the combination of blue skin and white underbelly of sharks via countershading (which makes them difficult to detect from both above and below). More complex patterns can be seen in animals such as flounder, moths, and frogs, among many others.

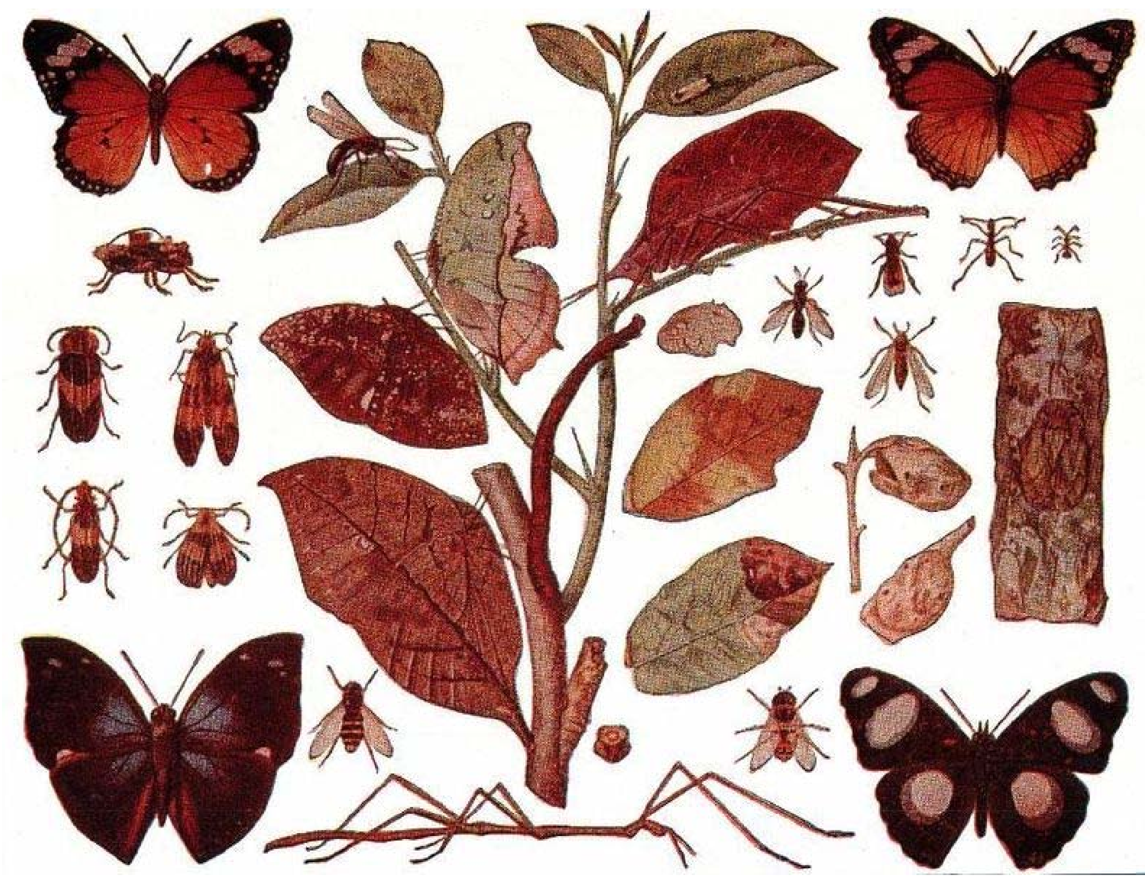
The type of camouflage a species will develop depends on several factors:

- The environment in which it lives. This is usually the most important factor.
- The physiology and behavior of an animal. Animals with fur need camouflage different from those with feathers or scales. Likewise, animals who live in groups use different camouflage techniques than those that are solitary.

- If the animal is preyed upon then the behavior or characteristics of its predator can influence how the camouflage develops. If the predator has achromatic vision, for example, then the animal will not need to match the color of its surroundings.

Animals produce colors in two ways:

- Biochromes: natural microscopic pigments that absorb certain wavelengths of light and reflect others, creating a visible color that is targeted towards its primary predator.
- Microscopic physical structures, which act like prisms to reflect and scatter light to produce a color that is different from the skin, such as the translucent fur of the Polar Bear, which actually has black skin.



Protective mimicry among insects

Cryptic coloration can change as well. This can be due to just a changing of the seasons, or it can be in response to more rapid environmental changes. For example, the Arctic fox has a white coat in winter, and a brown coat in summer. Mammals and birds require a new fur coat and new set of feathers respectively, but some animals, such as cuttlefish, have deeper-level pigment cells, called chromatophores, that they can control. Other animals such as certain fish species or the nudibranch can actually change their skin coloration by changing their diet. However, the most well-known creature that changes color, the chameleon, usually does not do so for camouflage purposes, but instead to express its mood.

Beyond colors, skin patterns are often helpful in cryptic coloration as well. The Cornsweet illusion describes visual perception as occurring through contrasts of outlines. One recognizes a dog, for example, not by its color as much as by its shape. Often what matters most for good cryptic coloration is to break up the outline of a creature's body. This can be seen in common domestic pets such as tabby cats, but striping overall in other animals such as tigers and zebras help them blend into their environment, the jungle and the grasslands respectively. The latter two provide an interesting example, as one's initial impression might be that their coloration does not match their surroundings at all, but tigers' prey are usually color blind to a certain extent such that they cannot tell the difference between orange and green, and zebras' main predators, lions, are color blind. In the case of zebras, the stripes also blend together so that a herd of zebras looks like one large mass, making it difficult for a lion to pick out any individual zebra. This same concept is used by many striped fish species as well. Among birds, the white "chinstraps" of Canada geese make a flock in tall grass appear more like sticks and less like birds' heads.

In nature, there is a strong evolutionary pressure for animals to blend into their environment or conceal their shape; for prey animals to avoid predators and for predators to be able to sneak up on prey. Natural camouflage is one method that animals use to meet these. There are a number of methods of doing so. One is for the animal to blend in with its surroundings, while another is for the animal to disguise itself as something uninteresting or something dangerous.

Hooded grasshopper

There is a permanent co-evolution of the sensory abilities of animals for whom it is beneficial to be able to detect the camouflaged animal, and the cryptic characteristics of the concealing species. Different aspects of crypsis and sensory abilities may be more or less pronounced in given predator-prey pairs of species.

Some cryptic animals also simulate natural movement, e.g., of a leaf in the wind. This is called procryptic behaviour or habit. Other animals attach or attract natural materials to their body for concealment. A few animals have chromatic response, changing color in changing environments, either seasonally (ermine, snowshoe hare) or far more rapidly with chromatophores in their integument (the cephalopod family). Some animals, notably in aquatic environments, also take steps to camouflage the odours they create that may attract predators. Some herd animals adopt a similar pattern to make it difficult to distinguish a single animal. Examples include stripes on zebras and the reflective scales on fish.

Gumleaf grasshopper, so named because of its mimicry of dead leaves

Hoplophrys oatesii crab hiding in a soft coral from East Timor.

An arctic hare's white colouration camouflages it in the snow

Camouflage allows predator to capture prey

The Egyptian Nightjar nests in the open sand with only its colouration to protect it

Scorpion fish resting beside a rope

A mackerel tabby cat blending with its (autumn) environment

Crab with red algae covering its body at Moss Beach, California

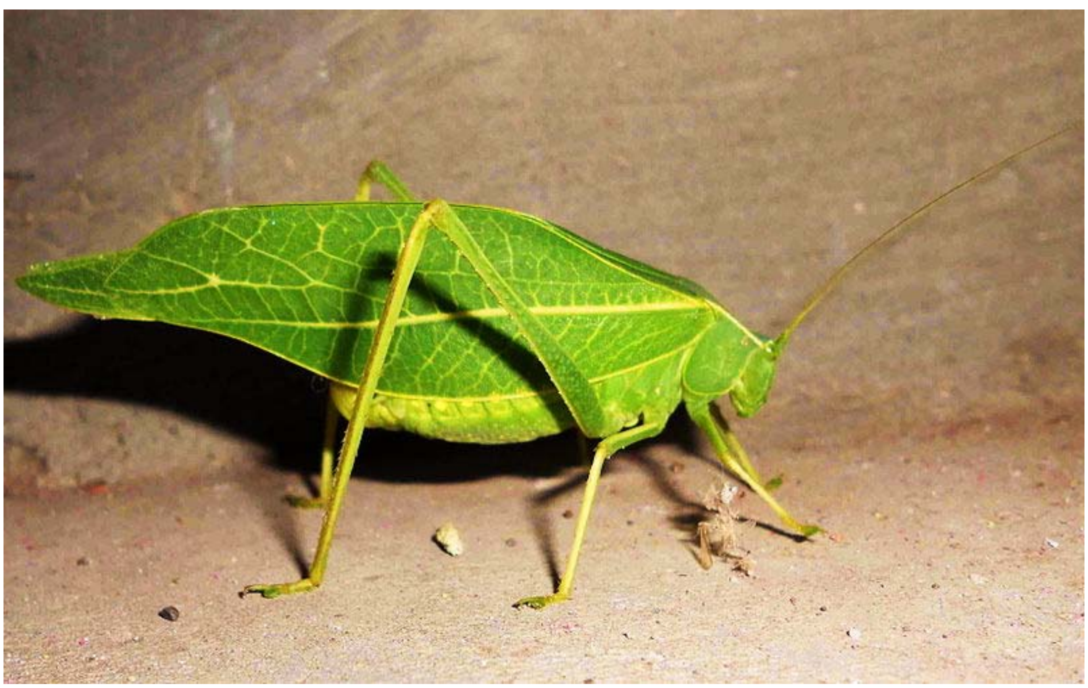
Countershaded Ibex are almost invisible in the Israeli desert.

A Bobcat blends with its winter surroundings, at Almaden Quicksilver County Park

Chameleon, Usambara mountains, Tanzania

Great male Leopard, made in Sabi Sands Private Game Reserve, South Africa

Tawny frogmouths in tree



Insect having mimicry of Green leaf

Zebras appear strikingly patterned to humans, but not to lions.

Chapter 7

Crypsis

This frog (facing right, on the upper left of the nearly-vertical stick on the rightmost third of the photo) is nearly invisible among the dead leaves in the Lower Rio Branco-Rio Jauaperi Extractive Reserve, Brazil.

The skin coloring of a Stenodactylus Sthenodactylus is well integrated with the coloring of the ground and rocks of the Judean desert

A common snakeneck turtle covered in camouflaging algae; when resting this individual would look like an algae-covered rock

Camouflaging allows animals to capture prey more easily.

In ecology, **crypsis** is the ability of an organism to avoid observation or detection by other organisms. A form of antipredator adaptation, methods range from camouflage, nocturnality, subterranean lifestyle, transparency, or mimicry. The word can also be used in the context of eggs and pheromone production.

Overview

There is a strong evolutionary pressure for animals to blend into their environment or conceal their shape; for prey animals to avoid predators and for predators to be able to sneak up on prey. (Exceptions include: large herbivores without natural enemies; brilliantly-colored birds which rely on flight to escape predators; and venomous or poisonous animals which advertise with bright colors.) Cryptic animals include the tawny frogmouth (feather patterning resembles bark), the tuatara (hides in burrows all day; nocturnal), some jellyfish (transparent), the leafy sea dragon, and the flounder (covers itself in sediment).

The distinction between camouflage and mimicry is arbitrarily defined in that mimicry requires that the "model" be another organism, rather than the surroundings; the distinction between the two phenomena can be seen by considering animals that resemble twigs, bark, leaves or flowers, in that they are often classified as camouflaged (a plant does constitute the "surroundings"), but sometimes classified as mimics (a plant is also an organism). Either way, the animal is considered cryptic.

Crypsis is usually most effective when an animal is still. Cryptic animals that forage during daylight may be ambush predators, taking advantage of their ability to blend into their background. Alternatively, cryptic animals may be active predators in darkness and use their crypsis while inactive. Some cryptic animals also simulate natural movement, e.g., of a leaf in the wind. This is called procryptic behaviour or habit. Other animals attach or attract natural materials to their body for concealment.

Varieties of crypsis

Crypsis may occur in a variety of ways, each of which causes the organism in question to blend with its background in at least one of the senses, although visual crypsis is the best known.

Visual

Many animals have evolved so that they visually resemble their surroundings, using some sort of natural camouflage that may match the color of the surroundings (cryptic coloration) and/or break up the visual outline of the animal itself. Such animals may resemble rocks, sand, twigs, leaves, and even bird droppings.

A few animals have chromatic response, changing color in changing environments, either seasonally (ermine, snowshoe hare) or far more rapidly with chromatophores in their integument (chameleon, cephalopods).

Countershading (or obliterative camouflage), the use of different colors on upper and lower surfaces in graduating tones from a light belly to a darker back, is common in the sea and on land. This is sometimes called Thayer's law, after Abbott H. Thayer who published a paper on the form in 1896.

Some animals, notably decorator crabs, attach other plants or animals to their bodies, allowing themselves to blend in with any environment, and even to change their camouflage.

Olfactory

Some animals, notably in aquatic environments, have adapted to camouflage the odours they create that may attract predators.

Effects

There is often a self-perpetuating co-evolution, or evolutionary arms race, between the perceptive abilities of animals for whom it is beneficial to be able to detect the cryptic animal, versus the cryptic characteristics of the hiding species. Different aspects of crypsis and sensory abilities may be more or less pronounced in given predator-prey species pairs.

Zoologists need special methods to study cryptic animals including biotelemetry techniques such as radio tracking, mark and recapture, and enclosures or exclosures.

Cryptic animals tend to be overlooked in studies of biodiversity and ecological risk assessment.

A ground agama (*Agama aculeata*), blending into his environment at the petrified forest, east of Doro !Nawas, Namibia.

An infant Cuttlefish blends into the surrounding sand substrate.

A Dead Leaf Mantis from Madagascar.

Tawny Frogmouth blends in with color and texture of tree bark.

Countershaded Ibex are almost invisible in the Israeli desert.

Australian grasshopper with the shape and coloration of a leaf

The colouration of the leaf-nosed viper (Eristicophis macmahonii) blends with sand.

Mossy leaf-tailed gecko (*Uroplatus sikorae*) blends with a log

A crab spider ambush hunting on a flower

Chapter 8

Interspecific Competition

Trees in this Bangladeshi forest are in competition for light.

Interspecific competition, in ecology, is a form of competition in which individuals of *different* species compete for the same resource in an ecosystem (e.g. food or living space). The other form of competition is intraspecific competition, which involves organisms of the same species.

If a tree species in a dense forest grows taller than surrounding tree species, it is able to absorb more of the incoming sunlight. However, less sunlight is then available for the trees that are shaded by the taller tree, thus interspecific competition. Cheetahs and lions can also be in interspecific competition, since both species feed on the same prey, and can be negatively impacted by the presence of the other because they will have less food.

Competition is only one of many interacting biotic and abiotic factors that affect community structure. Moreover, competition is not always a straightforward, direct, interaction. Interspecific competition may occur when individuals of two separate species share a limiting resource in the same area. If the resource cannot support both populations, then lowered fecundity, growth, or survival may result in at least one species. Interspecific competition has the potential to alter populations, communities and the evolution of interacting species. On an individual organism level, competition can occur as interference or exploitative competition.

Direct competition has been observed between individuals, populations and species, but there is little evidence that competition has been the driving force in the evolution of large groups. For example, between amphibians, reptiles and mammals.

Mechanisms

Interference competition

Interference competition involves direct interactions between individuals such as fighting over limited resources. This form of competition is typically, though not always, detrimental to both individuals and both species involved. These interactions are usually asymmetric with one species having an advantage over the other, resulting in greater loss by one competitor. For example, large predators like canids have a significant size advantage over smaller predators such as foxes or weasels. A violent interaction between two of these species would likely result in victory for the larger predator. The stability of some mammalian carnivore populations is maintained through these conflicts over prey resources.

An example of interference competition in which only one party is negatively affected is allelopathy, in which plants of one species release toxic chemicals that inhibit the germination and survival of other potential competitors. Some animals utilize a similar strategy. For example, algae in the feces of the common frog, *Rana temporaria*, inhibit the tadpoles of the competing natterjack toad, *Bufo calamita*.

Exploitative competition

Exploitative competition is a form of competition in which one species either reduces or more efficiently uses a resource and therefore depletes the availability of the resource for the other species. A good example of exploitative competition is found in aphid species competing over the sap in plant phloem. Each aphid species that feeds on host plant sap uses some of the resource, leaving less for competing species. In one study, *Fordinae geoica* was observed to out-compete *F. formicaria* to the extent that the latter species exhibited a reduction in survival by 841%.

This type of competition can also be observed in forests where large trees dominate the canopy and thus allow little light to reach smaller competitors living below. These interactions have important implications for the population dynamics and distribution of both species.

Apparent competition

Apparent competition occurs when two or more species in a habitat affect shared natural enemies in a higher trophic level. If two species share a common predator, for example, apparent competition can exist between the two prey items as they attempt to make themselves less available for consumption.

Scramble competition

Scramble competition occurs when a resource is inadequate for the needs of all. Each competitor obtains an equal amount, but never the amount it needs, leading to a depression in population growth.

Consequences

Many studies, including those cited previously, have shown major impacts on both individuals and populations from interspecific competition. Documentation of these impacts has been found in species from every major branch of organism. The effects of interspecific competition can also reach communities and can even influence the evolution of species as they adapt to avoid competition. This evolution may result in the exclusion of a species in the habitat, niche separation, and local extinction. The changes of these species over time can also change communities as other species must adapt.

Competitive exclusion

The competitive exclusion principle states that two species that use the same resource in the same way in the same space and time cannot coexist and must diverge from each other over time in order for the two species to coexist. One species will often exhibit an advantage in resource use. This superior competitor will out-compete the other with more efficient use of the limiting resource. As a result, the inferior competitor will suffer a decline in population over time. It will be excluded from the area and replaced by the superior competitor.

A well documented example of competitive exclusion was observed to occur between Dolly Varden charr (*Salvelinus malma*) and white spotted char (*S. leucomaenis*) in Japan.

Both of these species were morphologically similar but the former species was found primarily at higher elevations than the latter. Although there was a zone of overlap, each species excluded the other from its dominant region by becoming better adapted to its habitat over time. In some such cases, each species gets displaced into an exclusive segment of the original habitat. Because each species suffers from competition, natural selection favors the avoidance of competition in such a way.

Niche differentiation

Niche differentiation is a process by which competitive exclusion leads to differences with in resource use. In the previous example, niche differentiation resulted in spatial displacement. In other cases it may result in other changes that also avoid competition. If competition avoidance is achievable, each species will occupy an edge of the niche and will become more specialized to that area thus minimizing competition. This phenomenon often results in the separation of species over time as they become more specialized to their edge of the niche, called niche differentiation. The species do not have to be in separate habitats however to avoid niche overlap. Some species adapt regionally to utilizing different resources than they ordinarily would in order to avoid competition.

There have been several well documented cases in birds where species that are very similar change their habitat use where they overlap. For example, they may consume different food resources or use different nesting habitat or materials. On the Galapagos Islands, finch species have been observed to change dietary specializations in just a few generations in order to utilize limited resources and minimize competition.

In some cases, third party species interfere to the detriment or benefit of the competing species. In a laboratory study, coexistence between two competing bacterial species was mediated by phage parasites. This type of interaction actually helped to maintain diversity in bacterial communities and has far reaching implications in medical research as well as ecology. Similar effects have been documented for many communities as a result of the action of a keystone predator that preys on a competitively superior species.

Local extinction

Although local extinction of one or more competitors has been less documented than niche separation or competitive exclusion, it does occur. In an experiment involving zooplankton in artificial rock pools, local extinction rates were significantly higher in areas of interspecific competition. In these cases, therefore, the negative effects are not only at the population level but also species richness of communities.

Impacts on communities

As mentioned previously, interspecific competition has great impact on community composition and structure. Niche separation of species, local extinction and competitive exclusion are only some of the possible effects. In addition to these, interspecific competition can be the source of a cascade of affects that build on each other. An example of such an effect is the introduction of an invasive species to the United States, Purple-loosestrife. This plant when introduced to wetland communities often outcompetes much of the native flora and decreases species richness, food and shelter to many other species at higher trophic levels. In this way, one species can influence the populations of many other species as well as through a myriad of other interactions. Because of the complicated web of interactions that make up every ecosystem and habitat, the results of interspecific competition are complex and site-specific.

Lotka-Volterra model

The impacts of interspecific competition on populations have been formalized in a mathematical model called the Lotka-Volterra equation, which creates a theoretical prediction of interactions. It combines the effects of each species on the other. These effects are calculated separately for the first and second population respectively:

$$dN_1/dt=r_1N_1((K_1-N_1-\alpha_{12}N_2)/K_1)$$

$$dN_2/dt=r_2N_2((K_2-N_2-\alpha_{21}N_1)/K_2)$$

In these formulae, **N** is the population size, **t** is time, **K** is the carrying capacity, **r** is the intrinsic rate of increase and **α** is the competition coefficient. The results show the effect that the other species has on the species being calculated. The results can be graphed to show a trend and possible prediction for the future of the species. One problem with this model is that certain assumptions must be made for the calculation to work. These include the lack of migration and constancy of the carrying capacities and competition coefficients of both species. The complex nature of ecology determines that these assumptions are rarely true in the field but the model provides a basis for improved understanding of these important concepts.

Chapter 9

Intraguild Predation

Intraguild predation, or IGP, is the killing and eating of potential competitors. This interaction represents a combination of predation and competition, because both species utilize the same prey resources and also benefit from preying upon one another.
Intraguild predation is common in nature and can be asymmetrical, in which one species feeds upon the other, or symmetrical, in which both species prey upon each other. Because the dominant intraguild predator gains the dual benefits of feeding and eliminating a potential competitor, IGP interactions can have significant effects on the structure of ecological communities.

Types

Intraguild predation can be classified as **asymmetrical** or **symmetrical**. In **asymmetrical** interactions one species consistently preys upon the other, while in **symmetrical** interactions both species prey equally upon each other. Intraguild predation can also be **age structured**, in which case the vulnerability of a species to predation is dependent on age and size, so only juveniles or smaller individuals of one of the predators are fed upon by the other. A wide variety of predatory relationships are possible depending on the symmetry of the interaction and the importance of age structure. IGP interactions can range from predators incidentally eating parasites attached to their prey to direct predation between two apex predators.

Ecology of intraguild predation

Intraguild predation is common in nature and widespread across communities and ecosystems. Intraguild predators must share at least one prey species and usually fall within the same trophic guild, and the degree of IGP depends on factors such as the size, growth, and population density of the predators, as well as the population density and behavior of their shared prey. When creating theoretical models for intraguild predation, the competing species are classified as the "top predator" or the "intermediate predator," (the species more likely to be preyed upon). In theory, intraguild predation is most stable if the top predator benefits strongly from feeding on the intermediate predator, and if the intermediate predator is a better competitor for the shared prey resource.
The ecological effects of intraguild predation include direct effects on the survival and distribution of the competing predators, as well as indirect effects on the abundance and

distribution of prey species and other species within the community. Because they are so common, IGP interactions are important in structuring communities. Intraguild predation may actually benefit the shared prey species by lowering overall predation pressure, particularly if the intermediate predator consumes more of the shared prey. Intraguild predation can also dampen the effects of trophic cascades by providing redundancy in predation: if one predator is removed from the ecosystem, the other is still consuming the same prey species. Asymmetrical IGP can be a particularly strong influence on habitat selection. Often, intermediate predators will avoid otherwise optimal habitat because of the presence of the top predator. Behavioral changes in intermediate predator distribution due to increased risk of predation can have a more significant influence on community structure than mortality caused by the top predators.

Examples

Terrestrial

Intraguild predation is well documented in terrestrial arthropods such as insects and arachnids. Hemipteran insects and larval lacewings both prey upon aphids, but the competing predators can cause high enough mortality among the lacewings to effectively relieve predation upon the aphids. Several species of centipede are considered to be intraguild predators. Among the most dramatic examples of intraguild predation are those between large mammalian carnivores. Large canines and felines are the mammal groups most often involved in IGP, with larger species such as lions and gray wolves preying upon smaller species such as foxes and lynx. In North America, coyotes function as intraguild predators of gray foxes and bobcats, and may exert a strong influence over the population and distribution of gray foxes. However, in areas where wolves have been reintroduced, coyotes become an intermediate predator and experience increased mortality and a more restricted range.

Aquatic/marine

Intraguild predation is also important in aquaitic and marine ecosystems. As top predators in most marine environments, sharks show strong IGP interactions, both between species of sharks and with other top predators like toothed whales. In tropical areas where multiple species of sharks may have significantly overlapping diets, the risk of injury or predation can determine the local range and available prey resources for different species. Large pelagic species such as blue and mako sharks are rarely observed feeding in the same areas as great white sharks, and the presence of white sharks will prevent other species from scavenging on whale carcasses. Intraguild predation between sharks and toothed whales usually involves large sharks preying upon dolphins and porpoises while also competing with them for fish prey, but orcas reverse this trend by preying upon large sharks while competing for large fish and seal prey.

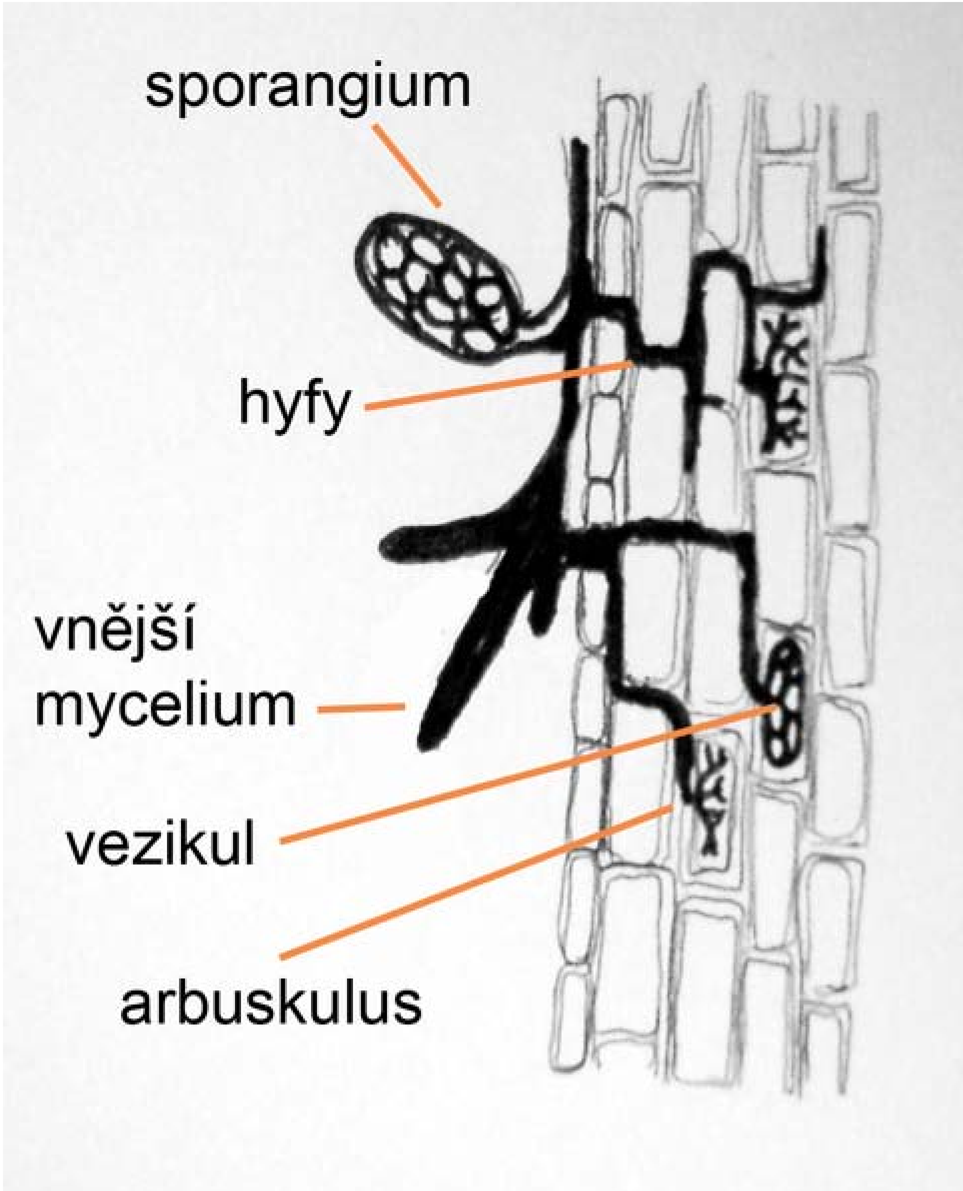
Importance to management and conservation

Knowledge of the presence and intensity of intraguild predation is important to both management and conservation of species. Human influence on communities and ecosystems can affect the balance of these interactions, and the direct and indirect effects of IGP may have economic consequences. Fisheries managers have only recently begun to understand the importance of intraguild predation on the availability of fish stocks as they attempt to move towards ecosystem-based management. IGP interactions between sharks and seals may prevent seals from feeding in areas where commercially-important fish species are abundant, which may indirectly make more of these fish available to fishermen. However, IGP may also negatively influence fisheries. Intraguild predation by spiny dogfish and various skate species on economically-important fishes like cod and haddock have been cited as a possible reason for the slow recovery of the groundfish fishery in New England. Intraguild predation is also an important consideration for restoring ecosystems. Because the presence of top predators can so strongly affect the distribution and abundance of both intermediate predator and prey species, efforts to either restore or control predator populations can have significant and often unintended ecological consequences. In Yellowstone National Park, the reintroduction of wolves caused them to become intraguild predators of coyotes, which had far-reaching effects on both the animal and plant communities in the park. Intraguild predation is an important ecological interaction, and conservation and management measures will need to take it into consideration.

Chapter 10

Mutualism (Biology)

Hummingbird Hawkmoth drinking from *Dianthus*. Pollination is a classic example of mutualism.



Arbuscular mycorrhiza

Mutualism is the way two organisms biologically interact where each individual derives a fitness benefit (i.e. increased reproductive output). Similar interactions within a species are known as co-operation. It can be contrasted with interspecific competition, in which each species experiences *reduced* fitness, and exploitation, or parasitism, in which one species benefits at the *expense* of the other. Mutualism and symbiosis are sometimes used as if they are synonymous, but this is strictly incorrect: symbiosis is a broad category, defined to include relationships which are mutualistic, parasitic or commensal. Mutualism is only one *type*.

A well known example of mutualism is the relationship between ungulates (such as cows) and bacteria within their intestines. The ungulates benefit from the cellulase produced by the bacteria, which facilitates digestion; the bacteria benefit from having a stable supply of nutrients in the host environment.

Mutualism plays a key part in ecology. For example, mutualistic interactions are vital for terrestrial ecosystem function as more than 48% of land plants rely on mycorrhizal relationships with fungi to provide them with inorganic compounds and trace elements.

In addition, mutualism is thought to have driven the evolution of much of the biological diversity we see, such as flower forms (important for pollination mutualisms) and co-evolution between groups of species. However mutualism has historically received less attention than other interactions such as predation and parasitism.

Measuring the exact fitness benefit to the individuals is not always straightforward, particularly when the individuals can receive benefits from a range of species, for example most plant-pollinator mutualisms. It is therefore common to categorise mutualisms according to the closeness of the association, using terms such as obligate versus facultative. Defining "closeness," however, is also problematic. It can refer to mutual dependency (the species cannot live without one another) or the biological intimacy of the relationship in relation to physical closeness (e.g. one species living within the tissues of the other species).

Types of relationships

Mutualistic transversals can be thought of as a form of "biological barter" in which species trade resources (for example carbohydrates or inorganic compounds) or services such as gamete, offspring dispersal, or protection from predators.

Resource-resource relationships

Resource-resource interactions, in which one type of resource is traded for a different resource, are probably the most common form of mutualism; for example mycorrhizal associations between plant roots and fungi, with the plant providing carbohydrates to the fungus in return for primarily phosphate but also nitrogenous compounds. Other examples include rhizobia bacteria which fix nitrogen for leguminous plants (family Fabaceae) in return for energy-containing carbohydrates.

Service-resource relationships

The Red-billed Oxpecker eats ticks on the impala's coat

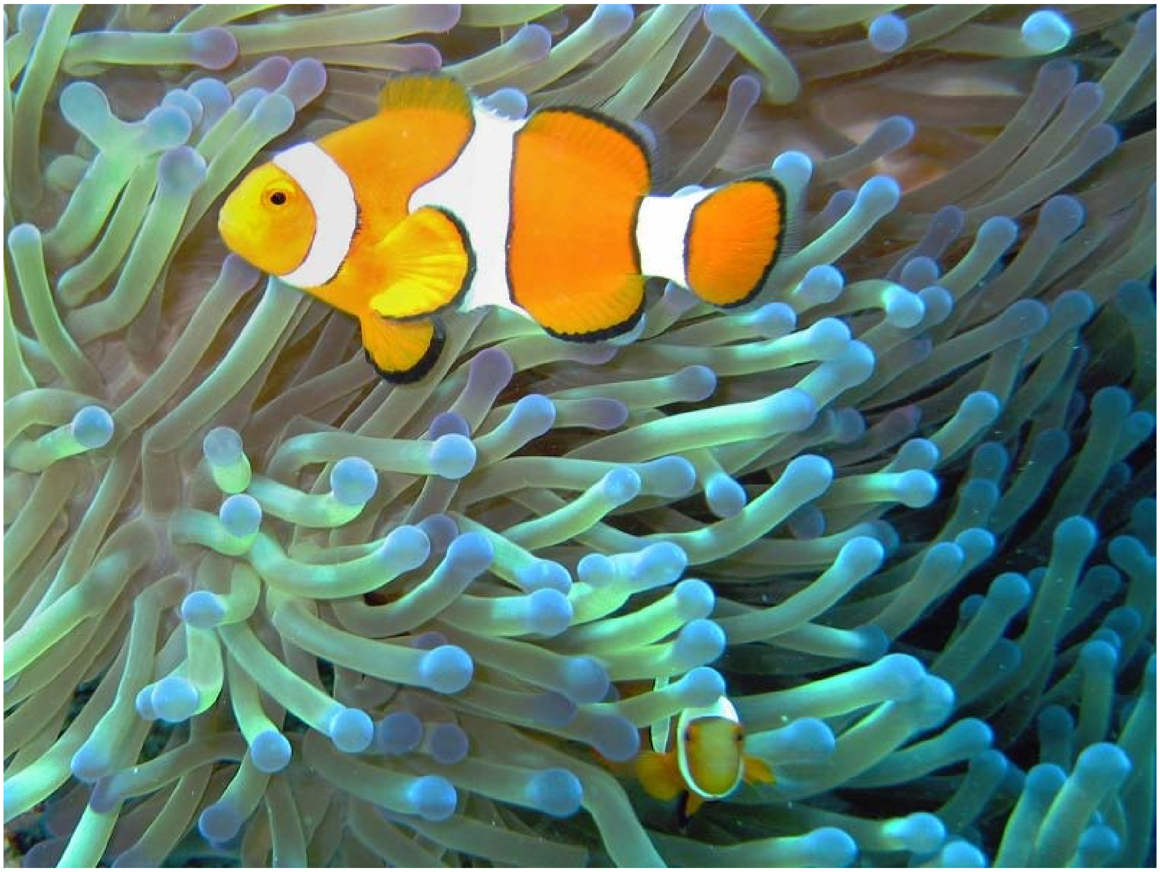
Service-resource relationships are also common.

Pollination in which nectar or pollen (food resources) are traded for pollen dispersal (a service) or ant protection of aphids, where the aphids trade sugar-rich honeydew (a by-product of their mode of feeding on plant sap) in return for defense against predators such as ladybird beetles.

Phagophiles feed (resource) on ectoparasites, thereby providing anti-pest service.

Zoochory is an example where animals disperse the seeds of plants. This is similar to pollination in that the plant produces food resources (for example, fleshy fruit, overabundance of seeds) for animals that disperse the seeds (service).

Service-service relationships



An example of mutual symbiosis is the relationship between Ocellaris clownfish that dwell among the tentacles of Ritteri sea anemones.

Strict service-service interactions are very rare, for reasons that are far from clear. One example is the relationship between sea anemones and anemonefish in the family Pomacentridae: the anemones provide the fish with protection from predators (which cannot tolerate the stings of the anemone's tentacles) and the fish defend the anemones against butterflyfish (family Chaetodontidae) which eat anemones. However, in common with many mutualisms, there is more than one aspect to it: in the anemonefish-anemone mutualism, waste ammonia from the fish feed the symbiotic algae that are found in the anemone's tentacles. Therefore what appears to be a service-service mutualism in fact has a service-resource component. A second example is that of the relationship between some ants in the genus *Pseudomyrmex* and trees in the genus *Acacia*, such as the Whistling Thorn and Bullhorn Acacia. The ants nest inside the plant's thorns. In exchange for shelter, the ants protect acacias from attack by herbivores (which they frequently eat, introducing a resource component to this service-service relationship) and competition from other plants by trimming back vegetation that would shade the acacia. In addition, another service-resource component is present, as the ants regularly feed on lipid-rich food-bodies called Beltian bodies that are on the *Acacia* plant.

In the Neotropics, the ant, *Myrmelachista schumanni* makes its nest in special cavities in *Duroia hirsute*. Plants in the vicinity which belong to other species are killed with formic acid. This selective gardening can be so aggressive that small areas of the rainforest are dominated by *Duroia hirsute*. These peculiar patches are known by local people as "devil's gardens".

In some of these relationships, the cost of the ant's protection can be quite expensive. *Cordia* sp. trees in the Amazonian rainforest have a kind of partnership with *Allomerus* sp. ants, which make their nests in modified leaves. To increase the amount of living space available, the ants will destroy the tree's flower buds. The flowers die and leaves develop instead, provisioning the ants with more dwellings. Another type of *Allomerus* sp. ant lives with the *Hirtella* sp. tree in the same forests, but in this relationship the tree has turned the tables on the greedy ants. When the tree is ready to produce flowers, the ant abodes on certain branches begin to wither and shrink, forcing the occupants to flee, leaving the tree's flowers to develop free from ant attack.

Humans and mutualism

Dogs and sheep were among the first animals to be domesticated.

Humans also engage in mutualisms with other species, including their gut flora (without which they would not be able to digest food efficiently) and domesticated animals such as horses, which provide transportation in return for food and shelter. In traditional agriculture, many plants will function mutualistically as companion plants, providing each other with shelter, soil fertility and the repelling of pests. For example, beans may grow up cornstalks as a trellis, while fixing nitrogen in the soil for the corn, as exploited in the Three Sisters gardening technique.

Mathematical theory

In 1989, David Hamilton Wright developed a mathematical explanation for mutualism using the Lotka–Volterra equation. Wright modified the Lotka-Volterra equations by adding a new term, βM/K, to represent a mutualistic relationship.

The mutalistic relationship is quantified by:

$dN/dt = r_1 N(1 – N/K1 + \beta_{12} M/K_1)$

$dM/dt = r_2 M (1 – M/K2 + \beta_{21} N/K_2)$

where,

- N and M = the population density
- r = intrinsic growth rate of the population
- K = carrying capacity of its local environmental setting.
- β = coefficient converting encounters with one species to new units of the other

Mutualism is essentially the logistic growth equation + mutualistic interaction. The mutualistic interaction term represents the increase in population growth of species one as a result of the presence of greater numbers of species two, and vice versa. Wright also considered the concept of saturation, which means that with higher densities, there are decreasing benefits of further increases of the mutualist population. Without saturation, species' densities would increase indefinitely. Because that isn't possible due to environmental constraints and carrying capacity, a model that includes saturation would be more accurate. Wright's mathematical theory is based on the premise of a simple two-species mutualism model in which the benefits of mutualism become saturated due to limits posed by handling time. Wright defines handling time as the time needed to process a food item, from the initial interaction to the start of a search for new food items and assumes that processing of food and searching for food are mutually exclusive. Mutualists that display foraging behavior are exposed to the restrictions on handling time. Mutualism can be associated with symbiosis

Type II functional response

In 1959, C. S. Holling performed his classic disc experiment that assumed the following: that (1), the number of food items captured is proportional to the allotted searching time; and (2), that there is a variable of handling time that exists separately from the notion of search time. He then developed an equation for the Type II functional response, which showed that the feeding rate is equivalent to

$ax/(1 + axT_H)$.

where,

- a = the instantaneous discovery rate
- x = food item density
- T_H = handling time

The equation that incorporates Type II functional response and mutualism is:

$$dN/dt = N\,[r(1-cN) + \beta M(X+M)]$$

where,

- N and M = density of the two mutualists
- r = intrinsic rate of increase of N
- c = coefficient measuring negative intraspecific interaction
- $X = 1/a\ T_H$
- $\beta = b/\ T_H$
- a = instantaneous discovery rate
- b = coefficient converting encounters with M to new units of N

Rearranged: $dN/dt = N[r(1-cN) + baM/(1+aT_HM)]$

These two graphs show the isoclines of mutualistic relationships. Presence of the mutualist has a positive effect on the recipient population at low densities of mutualists but at high densities, saturation takes place, and further increases in mutualist populations have little effect. Arrows indicate the stability or instability of equilibrium points.

Graph A illustrates a facultative mutualism in which both species derive benefits from each other, but do not depend on the existence of the other for survival.

Graph B demonstrates an obligate mutualism in which both species are interdependent on each other in a way that one species cannot survive without the other. Once the population of one species drops below the first equilibrium point, both populations will go extinct.

The model presented above is most effectively applied to free-living species that encounter a number of individuals of the mutualist part in the course of their existences. Of note, as Wright points out, is that models of biological mutualism tend to be similar qualitatively, in that the featured isoclines generally have a positive decreasing slope, and by and large similar isocline diagrams. Mutualistic interactions are best visualized as positively sloped isoclines, which can be explained by the fact that the saturation of benefits accorded to mutualism or restrictions posed by outside factors contribute to a decreasing slope.

Chapter 11

Mimicry

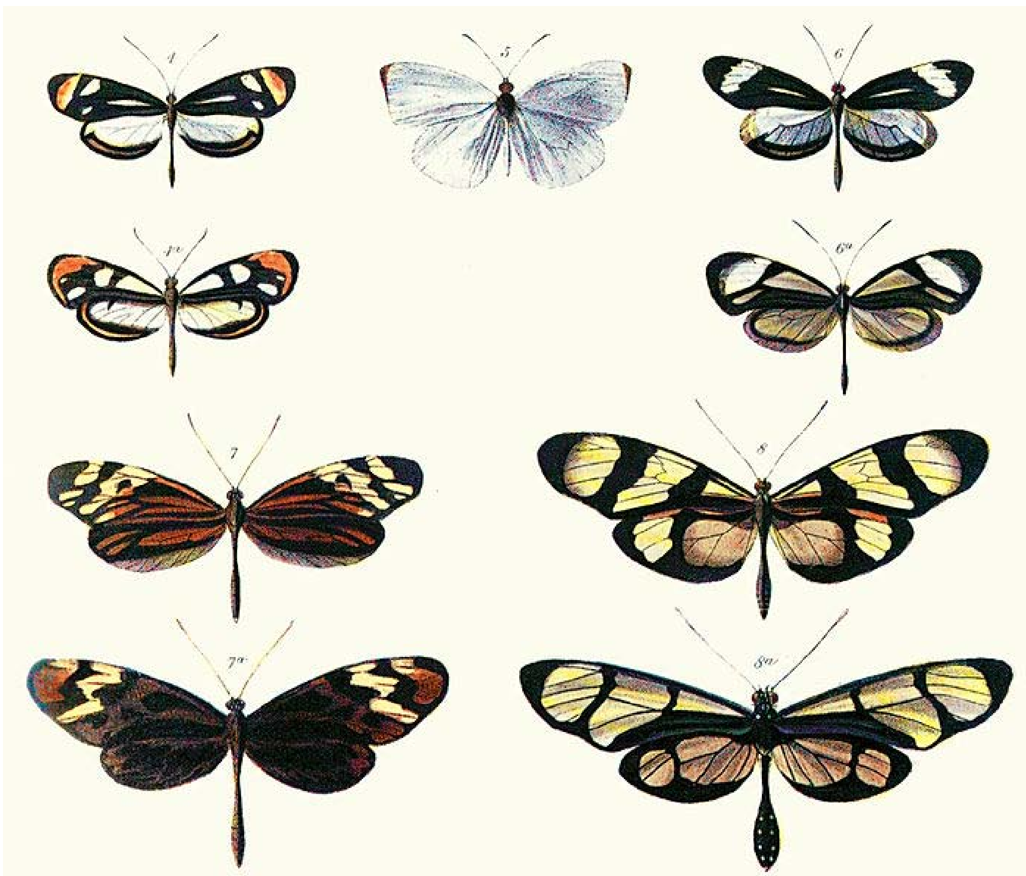


Plate from Henry Walter Bates (1862) illustrating Batesian mimicry between *Dismorphia* species (top row, third row) and various *Ithomiini* (Nymphalidae, second row, bottom row)

In evolutionary biology, **mimicry** is the similarity of one species to another which protects one or both. This similarity can be in appearance, behaviour, sound, scent and even location, with the mimics found in similar places to their models.

Mimicry occurs when a group of organisms, the *mimics*, evolve to share common perceived characteristics with another group, the *models*. The evolution is driven by the selective action of a *signal-receiver*, or *dupe*. For example, birds that use sight to identify palatable insects (the mimics), whilst avoiding the noxious models.

Collectively, this situation is known as a *mimicry complex*. The model is usually another species except in cases of automimicry. The signal-receiver is typically another intermediate organism like the common predator of two species, but may actually be the model itself, such as a moth resembling its spider predator. As an interaction, mimicry is in most cases advantageous to the mimic and harmful to the receiver, but may increase, reduce or have no effect on the fitness of the model depending on the situation. Models themselves are difficult to define in some cases, for example eye spots may not bear resemblance to any specific organism's eyes, and camouflage often cannot be attributed to a particular model.

A planthopper mimics a leaf (mimesis)

Camouflage, in which a species resembles its surroundings, is essentially a form of visual mimicry. In between camouflage and mimicry is **mimesis**, in which the mimic takes on the properties of a specific object or organism, but one to which the dupe is indifferent. The lack of a true distinction between the two phenomena can be seen in animals that resemble twigs, bark, leaves or flowers, in that they are often classified as camouflaged (a plant constitutes its "surroundings"), but are sometimes classified as mimics (a plant is also an organism). Crypsis is a broader concept which encompasses all forms of avoiding detection, such as mimicry, camouflage, hiding etc.

Though visual mimicry is most obvious to humans, other senses such as olfaction (smell) or hearing may be involved, and more than one type of signal may be employed. Mimicry may involve morphology, behavior, and other properties. In any case, the signal always functions to deceive the receiver by preventing it from correctly identifying the mimic. In evolutionary terms, this phenomenon is a form of co-evolution usually involving an evolutionary arms race. It should not be confused with convergent evolution, which occurs when species come to resemble one another *independently* by adapting to similar lifestyles.

Mimics may have different models for different life cycle stages, or they may be polymorphic, with different individuals imitating different models. Models themselves may have more than one mimic, though frequency dependent selection favors mimicry where models outnumber mimics. Models tend to be relatively closely related organisms, but mimicry of vastly different species is also known. Most known mimics are insects, though many other animal mimics including mammals are known. Plants and fungi may also be mimics, though less research has been carried out in this area.

Etymology

Use of the word mimicry dates back to 1637. It is derived from the Greek term *mimetikos*, "imitative," in turn from *mimetos*, the verbal adjective of *mimeisthai*, "to imitate." Originally used to describe people, it was only applied to other forms of life after 1851.

Classification

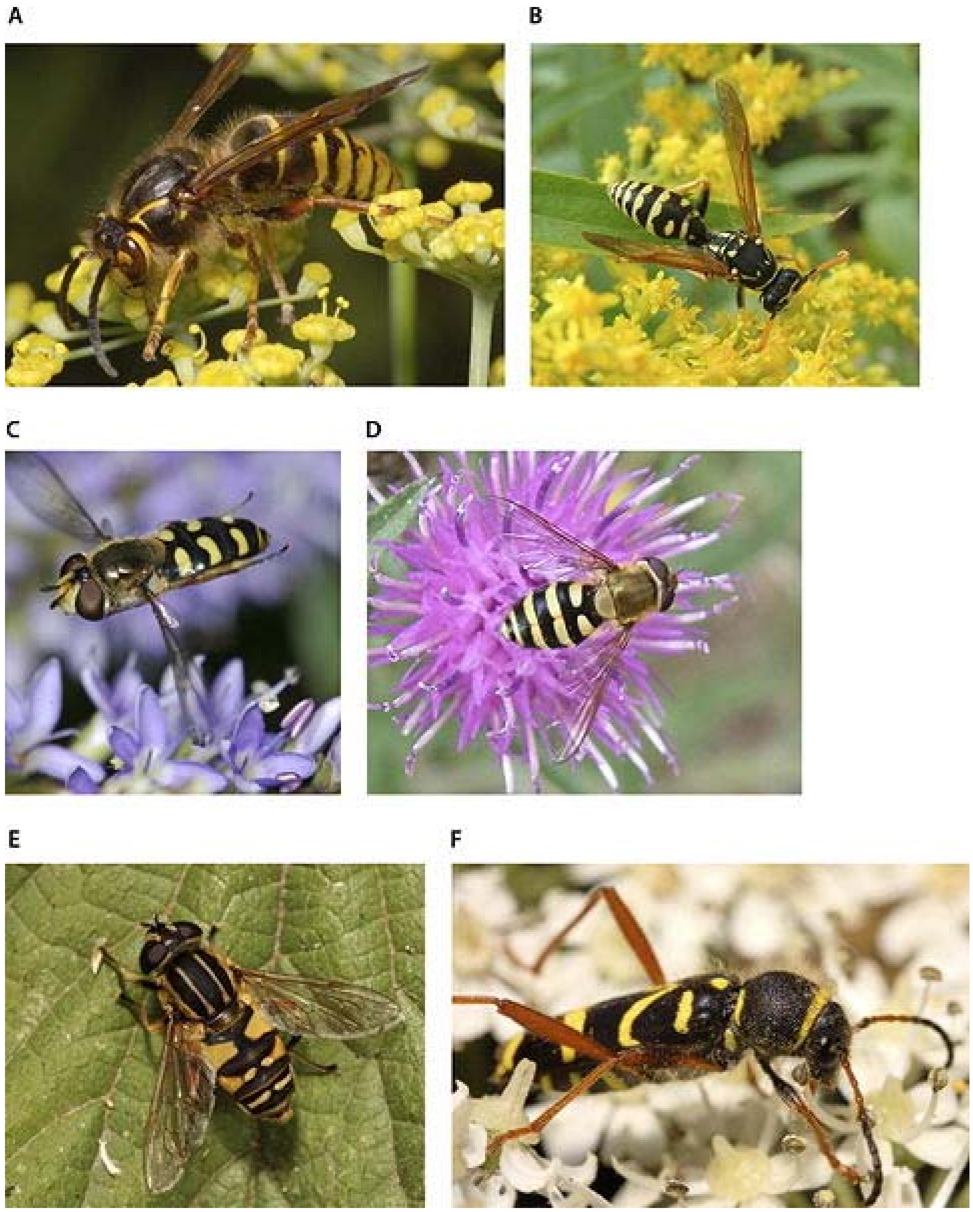
Many types of mimicry have been described. An overview of each follows, highlighting the similarities and differences between the various forms. Classification is often based on function with respect to the mimic (e.g. avoiding harm), though other parameters can also be used, and multidimensional classifications are required to understand the full picture. For this reason, some cases may belong to more than one class, e.g. automimicry and aggressive mimicry are not mutually exclusive, as one describes the species relationship between model and mimic, while the other describes the function for the mimic (obtaining food).

Defensive

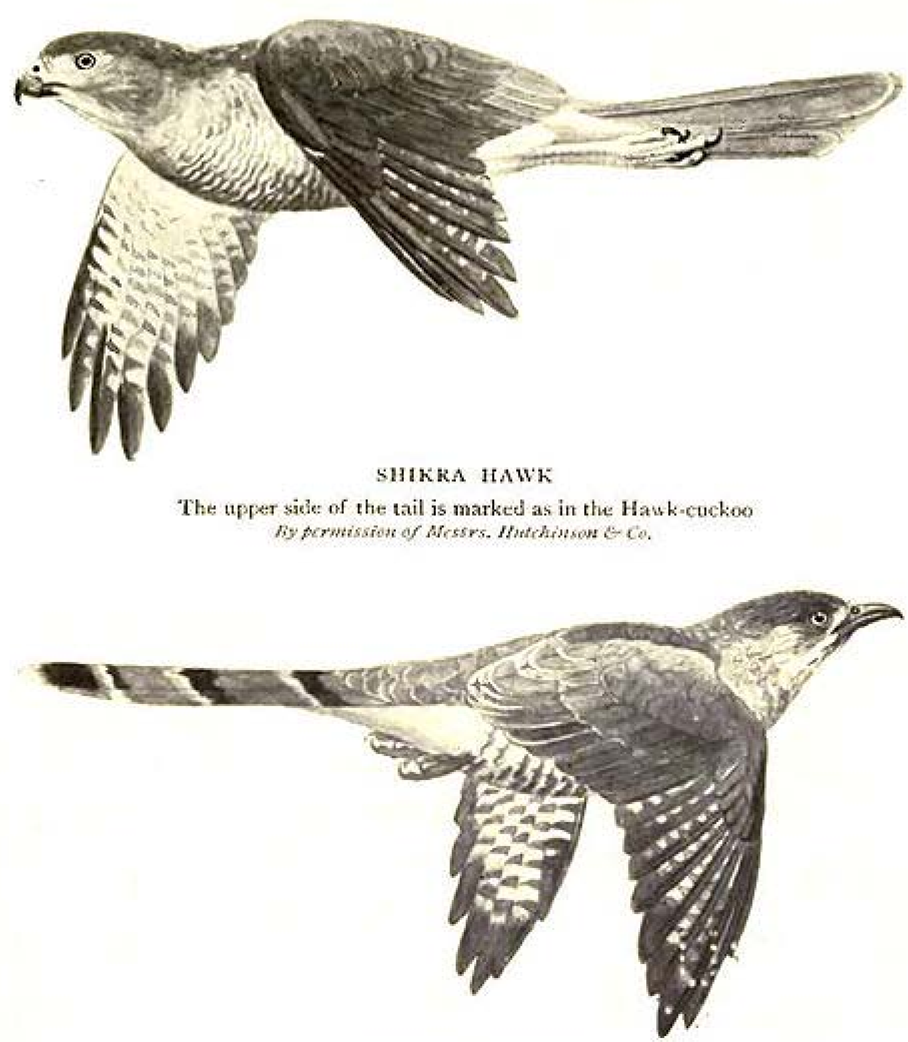
Macroxiphus sp katydid mimics an ant

Defensive or protective mimicry takes place when organisms are able to avoid an encounter that would be harmful to them by deceiving an enemy into treating them as something else. Four such cases are discussed here, the first three of which entail mimicry of an aposematic, harmful organism: Batesian mimicry, where a harmless mimic poses as harmful; Müllerian mimicry, where two harmful species share similar perceived characteristics; and Mertensian mimicry, where a deadly mimic resembles a less harmful but lesson-teaching model. Finally, Vavilovian mimicry, where weeds resemble crops, is discussed.

Batesian



Several species, including several hoverflies, mimic stinging species of wasp.



SHIKRA HAWK
The upper side of the tail is marked as in the Hawk-cuckoo
By permission of Messrs. Hutchinson & Co.

BRAIN-FEVER BIRD
The exact correspondence of this mimic with its model is notable even in black-and-white
By permission of Messrs. Hutchinson & Co.

Some hawk-cuckoos resemble hawks like the Shikra.

In Batesian mimicry the mimic shares signals similar to the model, but does not have the attribute that makes it unprofitable to predators (e.g. unpalatability). In other words, a Batesian mimic is a sheep in wolf's clothing. It is named after Henry Walter Bates, an English naturalist whose work on butterflies in the Amazon rainforest (including *Naturalist on the River Amazons*) was pioneering in this field of study. Mimics are less likely to be found out when in low proportion to their model, a phenomenon known as negative frequency dependent selection which applies in most other forms of mimicry as well. This is not the case in Müllerian mimicry however, which is described next. Examples:

- Lepidoptera

    - The Ash Borer (*Podosesia syringae*), a moth of the Clearwing family (Sesiidae), is a Batesian mimic of the Common wasp because it resembles the wasp, but is not capable of stinging. A predator that has learned to avoid the wasp would similarly avoid the Ash Borer.
    - Plain Tiger (*Danaus chrysippus*) – an unpalatable model with a number of mimics.
    - Common Crow (*Euploea core*) – an unpalatable model with a number of mimics.
    - *Consul fabius* and *Eresia eunice* imitate unpalatable *Heliconius* butterflies such as *H. ismenius*.
    - Several palatable butterflies resemble different species from the highly noxious papilionine genus *Battus*.
    - Several palatable moths produce ultrasonic click calls to mimic the unpalatable tiger moths.
- The False Cobra (*Malpolon moilensis*) is a mildly venomous but harmless colubrid snake which mimics the characteristic "hood" of an Indian cobra's threat display. The Eastern Hognose Snake (*Heterodon platirhinos*) similarly mimics the threat display of venomous snakes.
- The milk snake resembles the deadly coral snake.
- Vespid wasps bear several harmless mimics including moths, beetles and hoverflies.
- Octopuses of the genus *Thaumoctopus* (the Mimic Octopus) are able to intentionally alter their body shape and color so that they resemble dangerous sea snakes or lionfish.

Müllerian

The Heliconius butterflies from the tropics of the Western Hemisphere are the classical model for Müllerian mimicry.

Müllerian mimicry describes a situation where two or more species have very similar warning or aposematic signals and both share genuine anti-predation attributes (e.g. being unpalatable). At first Bates could not explain why this should be so; if both were harmful why did one need to mimic another? The German naturalist Fritz Müller put forward the first explanation for this phenomenon: If two species were confused with one another by a common predator, individuals in both would be more likely to survive. This type of mimicry is unique in several respects. Firstly, both the mimic and the model benefit from the interaction, which could thus be classified as mutualism in this respect. The signal receiver is also advantaged by this system, despite being deceived regarding species identity, as it avoids potentially harmful encounters. The usually clear identity of mimic and model are also blurred. In cases where one species is scarce and another abundant, the rare species can be said to be the mimic. When both are present in similar numbers however it is more realistic to speak of each as *comimics* than of a distinct 'mimic' and 'model' species, as their warning signals tend to converge toward something intermediate between the two. Another theoretical problem comes up when one considers that the two species may exist on a continuum from the harmless to the highly noxious, raising the question of where Batesian mimicry ends and Müllerian convergence begins.

Examples:

- Lepidoptera
  - The Monarch Butterfly (*Danaus plexippus*) is a member of a Müllerian complex with the Viceroy butterfly (*Limenitis archippus*) in shared coloration patterns and display behavior. The Viceroy has subspecies with somewhat different coloration, each one very closely matching the local *Danaus* species. E.g., in Florida, the pairing is of the Viceroy and the Queen Butterfly, and in Mexico, the Viceroy resembles the Soldier Butterfly. Therefore, the Viceroy is a single species involved in three different Müllerian pairs. This example was long believed to be a case of Batesian mimicry, with the Viceroy being the mimic and the Monarch the model, but it was more recently determined that the Viceroy is actually the *more* unpalatable species, though there is considerable individual variation. While *L. archippus* is really bad-tasting, *Danaus* species tend to be toxic rather than just repugnant, due to their different food plants.
  - Unpalatable *Euploea* species look very similar.
  - The genus *Morpho* is palatable but are very strong fliers; birds – even species which are specialized for catching butterflies on the wing – find it very hard to catch them. The conspicuous blue coloration shared by most *Morpho* species seems to be a case of Müllerian mimicry.
  - The "orange complex" of species, including the heliconiines *Agraulis vanillae*, *Dryadula phaetusa*, and *Dryas iulia* which all taste bad.
  - Many different tiger moths make ultrasonic clicking calls to warn bats that they are unpalatable. Presumably a bat may learn to avoid *any* signalling moths, which would make this an example of Müllerian mimicry.
- Various bees and numerous vespid and sphecoid wasps: These animals are examples of Müllerian mimics because they have the aposematic yellow and black stripes (sometimes black and red, or black and white). Females of most of these species are potentially harmful to predators, fulfilling the second requirement of Müllerian mimicry. However, in essentially all such species, the males are harmless, and can thus be considered automimics of their conspecific females (see below). There are also many genera in these groups where the females are not capable of stinging, and yet still possess aposematic coloration (e.g., the wasp genus *Cerceris*), so they are considered Batesian mimics.

Emsleyan/Mertensian

Texas Coral Snake, *Micrurus tener* (left) and Mexican Milk Snake, *Lampropeltis triangulum annulata* (right).

Emsleyan or *Mertensian mimicry* describes unusual cases where deadly prey mimic a less dangerous species. It was first proposed by Emsley as a possible answer for the problem of Coral Snake mimicry in the New World. It was elaborated on by the German biologist Wolfgang Wickler in a chapter of *Mimicry in Plants and Animals*, who named it after the German herpetologist Robert Mertens. Sheppard points out that Hecht and Marien put forward a similar hypothesis ten years earlier.

This scenario is a little more difficult to understand, as in other types of mimicry it is usually the most harmful species that is the model. But if a predator dies, it cannot learn to recognize a warning signal, e.g. bright colors in a certain pattern. In other words, there is no advantage in being aposematic for an organism that is likely to kill any predator it succeeds in poisoning; such an animal would rather profit from being camouflaged, to avoid attacks altogether. If, however, there is some other species that is harmful but *not* deadly as well as aposematic, the predator may learn to recognize its particular warning colors and avoid such animals. A deadly species will then profit by mimicking the less dangerous aposematic organism, if this results in less attacks than camouflage would.

The exception here, ignoring any chance of animals learning by watching a conspecific die, is the possibility of not having to learn that it is harmful in the first place: instinctive genetic programming to be wary of certain signals. In this case, other organisms could benefit from this programming, and Batesian or Müllerian mimics of it could potentially evolve. In fact, it has been shown that some species do have an innate recognition of certain aposematic warnings. Hand-reared Turquoise-browed Motmots (*Eumomota superciliosa*), avian predators, instinctively avoid snakes with red and yellow rings. Other colors with the same pattern, and even red and yellow *stripes* with the same width as rings, were tolerated. However, models with red and yellow rings were feared, with the birds flying away and giving alarm calls in some cases. This provides one alternative explanation to Mertensian mimicry.

Examples:

- Some Milk Snake (*Lampropeltis triangulum*) subspecies (harmless), the moderately toxic False Coral Snakes (genus *Erythrolamprus*), and the deadly Coral Snakes all have a red background color with black and white/yellow rings.

In this system, both the milk snakes and the deadly coral snakes are mimics, whereas the false coral snakes are the model.

Wasmannian

Wasmannian mimicry refers to cases where the mimic resembles a model along with which it lives (inquiline) in a nest or colony. Most of the models here are social insects such as ants, termites, bees and wasps.

Mimetic weeds

Rye is a secondary crop, originally being a mimetic weed of wheat.

Vavilovian mimicry describes weeds which come to share characteristics with a domesticated plant through artificial selection. It is named after Russian botanist and geneticist Nikolai Vavilov. Selection against the weed may occur either by manually killing the weed, or separating its seeds from those of the crop. The latter process, known as winnowing, can be done manually or by a machine.

Vavilovian mimicry presents an illustration of unintentional (or rather 'anti-intentional') selection by man. While some cases of artificial selection go in the direction desired, such as selective breeding, this case presents the opposite characteristics. Weeders do not want to select weeds that look increasingly like the cultivated plant, yet there is no other option. A similar problem in agriculture is pesticide. Vavilovian mimics may eventually be domesticated themselves, and Vavilov called these weeds-cum-crops *secondary crops*.

It can be classified as defensive mimicry in that the weed mimics a protected species. This bears strong similarity to Batesian mimicry in that the weed does not share the properties that give the model its protection, and both the model and the dupe (in this case people) are harmed by its presence. There are some key differences, though; in Batesian mimicry the model and signal receiver are enemies (the predator would eat the protected species if could), whereas here the crop and its human growers are in a mutualistic relationship: the crop benefits from being dispersed and protected by people, despite being eaten by them. In fact, the crop's only 'protection' relevant here is its usefulness to humans. Secondly, the weed is not eaten, but simply destroyed. The only motivation for killing the weed is its effect on crop yields. Finally, this type of mimicry does not occur in ecosystems unaltered by humans.

One case is *Echinochloa oryzoides*, a species of grass which is found as a weed in rice (*Oryza sativa*) fields. The plant looks similar to rice and its seeds are often mixed in rice and difficult to separate. This close similarity was enhanced by the weeding process which is a selective force that increases the similarity of the weed in each subsequent generation.

Protective egg decoys

Unlike the above forms of mimicry, *Gilbertian mimicry* involves only two species. The potential host/prey drives away its parasite/predator by mimicking it, the reverse of host-parasite aggressive mimicry. It was coined by Pasteur as a term for such rare mimicry systems, and is named after the American ecologist Lawrence E. Gilbert.

This form of protective mimicry occurs in the genus *Passiflora*. The leaves of this plant contain toxins which deter herbivorous animals, however some *Heliconius* butterfly larvae have evolved enzymes which break down these toxins, allowing them to specialize on this genus. This has created further selection pressure on the host plants, which have evolved stipules that mimic mature *Heliconius* eggs near the point of hatching. These butterflies tend to avoid laying eggs near each existing ones, which helps avoid exploitative intraspecific competition between caterpillars—those that lay on vacant leaves provide their offspring with a greater chance of survival. Additionally, most *Heliconius* larvae are cannibalistic, meaning those leaves with older eggs will hatch first and eat the new arrivals. Thus, it seems such plants have evolved egg dummies due to these grazing herbivore enemies. The decoy eggs are also nectaries though, attracting predators of the caterpillars such as ants and wasps. The extent of their mimetic function is therefore slightly more difficult to assess.

The use of eggs is not essential to this system, only the species composition and protective function. Many other forms of mimicry also involve eggs, such as cuckoo eggs mimicking those of their host (the reverse of this situation), or plants seeds (often those with an elaiosome) being dispersed by ants, who treat them as they would their own eggs.

Protective mimicry within a species

Monarch caterpillars, shown feeding, vary in toxicity depending on their diet.

Browerian mimicry, named after Lincoln P. Brower and Jane Van Zandt Brower, is a form of *automimicry*; where the model belongs to the same species as the mimic. This is the analogue of Batesian mimicry within a single species, and occurs when there is a palatability spectrum within a population. One example is Monarch Butterflies (*Danaus plexippus*), which feed on milkweed species of varying toxicity. This species stores toxins from its host plant, which are maintained even in the adult (imago) form. As the levels of toxin will vary depending on diet during the larval stage, some individuals will be more toxic than others. The less palatable organisms will therefore be mimics of the more dangerous individuals, with their likeness already perfected. This need not be the case however; in sexually dimorphic species one sex may be more of a threat than the other, which could mimic the protected sex. Evidence for this possibility is provided by the behavior of a monkey from Gabon, which regularly ate male moths of the genus *Anaphe*, but promptly stopped after it tasted a noxious female.

Aggressive

Aggressive mimicry describes predators (or parasites) which share the same characteristics as a harmless species, allowing them to avoid detection by their prey (or host). The mimic may resemble the prey or host itself, or another organism which is either neutral or beneficial to the signal receiver. In this class of mimicry the model may be affected negatively, positively or not at all. Just as parasites can be treated as a form of predator, host-parasite mimicry is treated here as a subclass of aggressive mimicry.

The mimic may have a particular significance for duped prey. One such case is spiders, amongst which aggressive mimicry is quite common in both luring prey and stealthily approaching predators. One case is the Golden Orb Weaver (*Nephila clavipes*), which spins a conspicuous golden colored web in well-lit areas. Experiments show that bees are able to associate the webs with danger when the yellow pigment is not present, as occurs in less well-lit areas where the web is much harder to see. Other colors were also learned and avoided, but bees seemed least able to effectively associate yellow pigmented webs with danger. Yellow is the color of many nectar bearing flowers, however, so perhaps avoiding yellow is not worth while. Another form of mimicry is based not on color but pattern. Species such as *Argiope argentata* employ prominent patterns in the middle of their webs, such as zigzags. These may reflect ultraviolet light, and mimic the pattern seen in many flowers known as nectar guides. Spiders change their web day to day, which can be explained by bee's ability to remember web patterns. Bees are able to associate a certain pattern with a spatial location, meaning the spider must spin a new pattern regularly or suffer diminishing prey capture.

Another case is where males are lured towards what would seem to be a sexually receptive female; the model in this situation being the same species as the dupe. Beginning in the 1960s, James E. Lloyd's investigation of female fireflies of the genus *Photuris* revealed they emit the same light signals that females of the genus *Photinus* use as a mating signal. Further research showed male fireflies from several different genera are attracted to these "femmes fatales", and are subsequently captured and eaten. Female signals are based on that received from the male, each female having a repertoire of signals matching the delay and duration of the female of the corresponding species. This mimicry may have evolved from non-mating signals that have become modified for predation.

The Spotted Predatory Katydid (*Chlorobalius leucoviridis*) is an acoustic aggressive mimic of cicadas.

The listrosceline katydid *Chlorobalius leucoviridis* of inland Australia is capable of attracting male cicadas of the Tribe Cicadettini by imitating the species-specific reply clicks of sexually receptive female cicadas. This example of acoustic aggressive mimicry is similar to the *Photuris* firefly case in that the predator's mimicry is remarkably versatile – playback experiments show that *C. leucoviridis* is able to attract males of many cicada species, including Cicadettine cicadas from other continents, even though cicada mating signals are species-specific.

Some carnivorous plants may also be able to increase their rate of capture through mimicry.

Two Bluestreak cleaner wrasse cleaning a Potato grouper, *Epinephelus tukula*

Luring is not a necessary condition however, as the predator will still have a significant advantage by simply not being identified as such. They may resemble a mutualistic symbiont or a species of little relevance to the prey.

A case of the former situation is a species of cleaner fish and its mimic, though in this example the model is greatly disadvantaged by the presence of the mimic. Cleaner fish are the allies of many other species, which allow them to eat their parasites and dead skin. Some allow the cleaner to venture inside their body to hunt these parasites. However, one species of cleaner, the Bluestreak cleaner wrasse (*Labroides dimidiatus*), is the unknowing model of a mimetic species, the Sabre-toothed blenny (*Aspidontus taeniatus*). This wrasse, shown to the left cleaning a grouper of the genus *Epinephelus*, resides in coral reefs in the Indian and the Pacific Oceans, and is recognized by other fishes who then allow it to clean them. Its imposter, a species of blenny, lives in the Indian Ocean and not only looks like it in terms of size and coloration, but even mimics the cleaner's 'dance'. Having fooled its prey into letting its guard down, it then bites it, tearing off a piece of its fin before fleeing the scene. Fish grazed upon in this fashion soon learn to distinguish mimic from model, but because the similarity is close between the two they become much more cautious of the model as well, such that both are affected. Due to victim's ability to discriminate between foe and helper, the blennies have evolved close similarity, right down to the regional level.

Another interesting example that does not involve any luring is the Zone-tailed Hawk, which resembles the Turkey Vulture. It flies amongst the vultures, suddenly breaking from the formation and ambushing its prey. Here the hawk's presence is of no evident significance to the vultures, affecting them neither negatively or positively.

Parasites

Parasites can also be aggressive mimics, though the situation is somewhat different from those outlined above.

Some of the predators described have a feature that draws prey, and parasites can also mimic their host's natural prey, but are eaten themselves, a pathway into their host. *Leucochloridium*, a genus of flatworm, matures in the digestive system of songbirds, their eggs then passing out of the bird via the feces. They are then taken up by *Succinea*, a terrestrial snail. The eggs develop in this intermediate host, and then must find of a suitable bird to mature in. As the host birds do not eat snails, so the sporocyst has another strategy to reach its host's intestine. They are brightly colored and move in a pulsating fashion. A sporocyst-sac pulsates in the snail's eye stalks, coming to resemble an irresistible meal for a songbird. In this way, it can bridge the gap between hosts, allowing it to complete its life cycle. A nematode (*Myrmeconema neotropicum*) changes the colour of the abdomen of workers of the canopy ant *Cephalotes atratus* to make it appear like the ripe fruits of *Hyeronima alchorneoides*. It also changes the behaviour of the ant so that the gaster (rear part) is held raised. This presumably increases the chances of the ant being eaten by birds. The droppings of birds are collected by other ants and fed to their brood, thereby helping to spread the nematode.

In an unusual case, planidium larvae of some beetles of the genus *Meloe* will form a group and produce a pheromone that mimics the sex attractant of its host bee species; when the male bee arrives and attempts to mate with the mass of larvae, they climb onto his abdomen, and from there transfer to a female bee, and from there to the bee nest to parasitize the bee larvae.

Host-parasite mimicry is a two species system where a parasite mimics its own host. Cuckoos are a canonical example of brood parasitism, a form of kleptoparasitism where the mother has its offspring raised by another unwitting organism, cutting down the biological mother's parental investment in the process. The ability to lay eggs which mimic the host eggs is the key adaptation. The adaptation to different hosts is inherited through the female line in so-called gentes. Cases of *intraspecific* brood parasitism, where a female lays in conspecific's nest, as illustrated by the Goldeneye duck (*Bucephala clangula*), do not represent a case of mimicry.

Reproductive

Reproductive mimicry occurs when the actions of the dupe directly aid in the mimic's reproduction. This is common in plants, which may have deceptive flowers that do not provide the reward they would seem to. Other forms of mimicry have a reproductive component, such as Vavilovian mimicry involving seeds, and brood parasitism, which also involves aggressive mimicry.

Mimicry of flowers

Bakerian mimicry, named after Herbert G. Baker, is a form of automimicry where female flowers mimic male flowers of their own species, cheating pollinators out of a reward. This reproductive mimicry may not be readily apparent as members of the same species may still exhibit some degree of sexual dimorphism. It is common in many species of Caricaceae.

Like Bakerian mimicry, *Dodsonian mimicry* is a form of reproductive floral mimicry, but the model belongs to a different species than the mimic. The name refers to Calaway H. Dodson. By providing similar sensory signals as the model flower, it can lure its pollinators. Like Bakerian mimics, no nectar is provided. *Epidendrum ibaguense* of the family Orchidaceae resembles flowers of *Lantana camara* and *Asclepias curassavica*, and is pollinated by Monarch Butterflies and perhaps hummingbirds. Similar cases are seen in some other species of the same family. The mimetic species may still have pollinators of its own though, for example a lamellicorn beetle which usually pollinates correspondingly colored *Cistus* flowers is also known to aid in pollination of *Ophrys* species that are normally pollinated by bees.

Pseudocopulation

The Fly Orchid (*Ophrys insectifera*)

Pseudocopulation occurs when a flower mimics a female of a certain insect species, the males of which try to copulate with it. This is much like the aggressive mimicry in fireflies described above, but with a much more benign outcome for the pollinator. This form of mimicry has been called *Pouyannian mimicry*, after Pouyanne, who first described the phenomenon. It is most common in orchids which mimic females of the order Hymenoptera (generally bees and wasps), and may account for around 60% of pollinations. Depending on the morphology of the flower, a pollen sac called a pollinia is attached to the head or abdomen of the male. This is then transferred to the stigma of the next flower the male tries to inseminate, resulting in pollination. Visual mimicry is the most obvious sign of this deception for humans, but the visual aspect may be minor or non-existent. It is the senses of touch and olfaction that are most important.

Inter-sexual mimicry

Inter-sexual mimicry occurs when individuals of one sex in a species mimic members of the opposite sex. An example is the three male forms of the marine isopod, *Paracerceis sculpta*. Alpha males are the largest and guard a harem of females. Beta males mimic females and manage to enter the harem of females without being detected by the alpha males allowing them to mate. Gamma males are the smallest males and mimic juveniles. This also allows them to mate with the females without the alpha males detecting them. Some male Australian Giant Cuttlefish also mimic females, allowing them to mate undetected by other males.

Automimicry

Automimicry or *intraspecific mimicry* occurs within a single species, one case being where one part of an organism's body resembles another part. Examples include snakes in which the tail resembles the head and show behavior such as moving backwards to confuse predators and insects and fishes with eyespots on their hind ends to resemble the head. The term is also used when the mimic imitates other morphs within the same species. When males mimic females or *vice versa* this may be referred to as sexual mimicry.

Examples:

- Many insects have filamentous "tails" at the ends of their wings which are combined with patterns of markings on the wings themselves to create a "false head" which misdirects predators (e.g., hairstreak butterflies).
- Several pygmy owls bear "false eyes" on the back of their head to fool predators into believing the owl is alert to their presence.
- The yellow throated males of the Common Side-blotched Lizard use a 'sneaking' strategy in mating. They look and behave like unreceptive females. This strategy is effective against 'usurper' males with orange throats, but ineffective against blue throated 'guarder' males, which will chase them away.
- Female hyenas have pseudo-penises which make them look like males.

Other

Some forms of mimicry do not fit easily within the classification given above.

Owl butterflies (genus *Caligo*) bear eye-spots on the underside of their wings; if turned upside-down, their undersides resemble the face of an owl (such as the Short-eared Owl or the Tropical Screech Owl) for which in turn the butterfly predators – small lizards and birds – would be fooled. Thus it has been supposed that the eye-spots are a form of Batesian mimicry. However, the pose in which the butterfly resembles an owl's head is not normally adopted in life. Research suggests that eye-spots are not a form of mimicry and do not deter predators because they look like eyes. Rather the conspicuous contrast in the patterns on the wings deter predators.

Another case is floral mimicry induced by the discomycete fungus *Monilinia vaccinii-corymbosi*. In this unusual case, a fungal plant pathogen infects leaves of blueberries, causing them to secrete sugary substances including glucose and fructose, in effect mimicking the nectar of flowers. To the naked eye the leaves do not look like flowers, yet strangely they still attract pollinating insects like bees. As it turns out, the sweet secretions are not the only cues—the leaves also reflect ultraviolet, which is normally absorbed by the plant's leaves. Ultraviolet light is also employed by the host's flowers as a signal to insects, which have visual systems quite capable of picking up this low wavelength (300–400 nm) radiation. The fungus is then transferred to the ovaries of the flower where it produces mummified, inedible berries, which overwinter before infecting new plants. This case is unusual in that the fungus benefits from the deception, but it is the leaves which act as mimics, being harmed in the process. It bears similarity to host-parasite mimicry, but the host does not receive the signal. It also has a little in common with automimicry, but the plant does not benefit from the mimicry, and the action of the pathogen is required to produce it.

Evolution

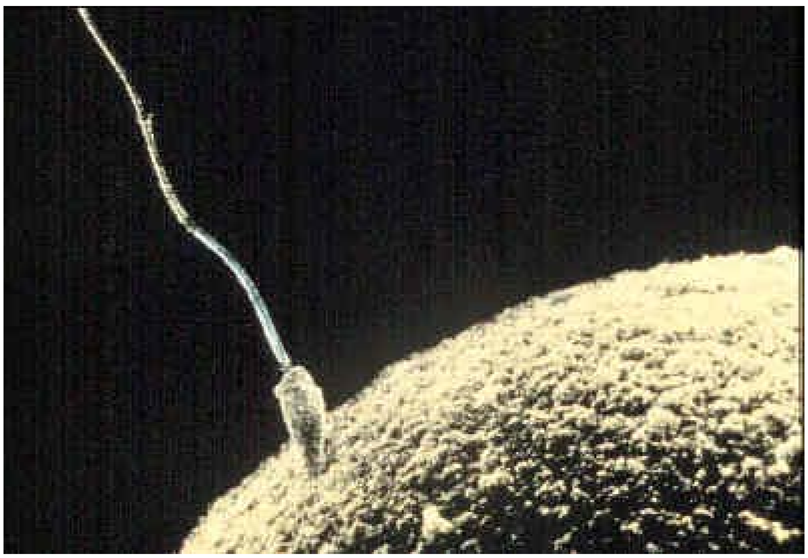
Ctenomorphodes chronus mimicking a eucalyptus twig

It is widely accepted that mimicry evolves as a positive adaptation; that is, the mimic gains fitness gradually *via* convergent evolution which results in resemblance to another species. The lepidopterist (and sometime author) Vladimir Nabokov argued that although natural selection might stabilize a "mimic" form, it would not be necessary to create it. It may be that much of insect mimicry, including the Viceroy/Monarch mimicry, results from similar self-organizing processes, and thus the tendency for convergence by chance would be high.

The most widely accepted model used to explain the evolution of mimicry in butterflies is the two-step hypothesis. In this model the first step involves mutation in modifier genes that regulate a complex cluster of linked genes associated with large changes in morphology. The second step consists of selections on genes with smaller phenotypic effects and this leading to increasing closeness of resemblance. This model is supported by empirical evidence that suggests that there are only a few single point mutations that cause large phenotypic effects while there are numerous others that produce smaller effects. Some regulatory elements are now known to be involved in a supergene that is involved in the development of butterfly color patterns. Computational simulations of population genetics have also supported this idea.

Chapter 12

Sex



Successful reproductive sex in animals results in the fusion of a sperm and egg cell.

In biology, **sex** is a process of combining and mixing genetic traits, often resulting in the specialization of organisms into a male or female variety (each known as a **sex**). Sexual reproduction involves combining specialized cells (gametes) to form offspring that inherit traits from both parents. Gametes can be identical in form and function (known as isogametes), but in many cases an asymmetry has evolved such that two sex-specific types of gametes (heterogametes) exist: male gametes are small, motile, and optimized to transport their genetic information over a distance, while female gametes are large, non-motile and contain the nutrients necessary for the early development of the young organism.

An organism's sex is defined by the gametes it produces: males produce male gametes (spermatozoa, or sperm) while females produce female gametes (ova, or egg cells); individual organisms which produce both male and female gametes are termed hermaphroditic. Frequently, physical differences are associated with the different sexes of an organism; these sexual dimorphisms can reflect the different reproductive pressures the sexes experience.

Evolution

It is considered that sexual reproduction first appeared about a billion years ago, evolved within ancestral single-celled eukaryotes. The reason for the initial evolution of sex, and the reason(s) it has survived to the present, are still matters of debate. Some of the many plausible theories include: that sex creates variation among offspring, sex helps in the spread of advantageous traits, and that sex helps in the removal of disadvantageous traits.

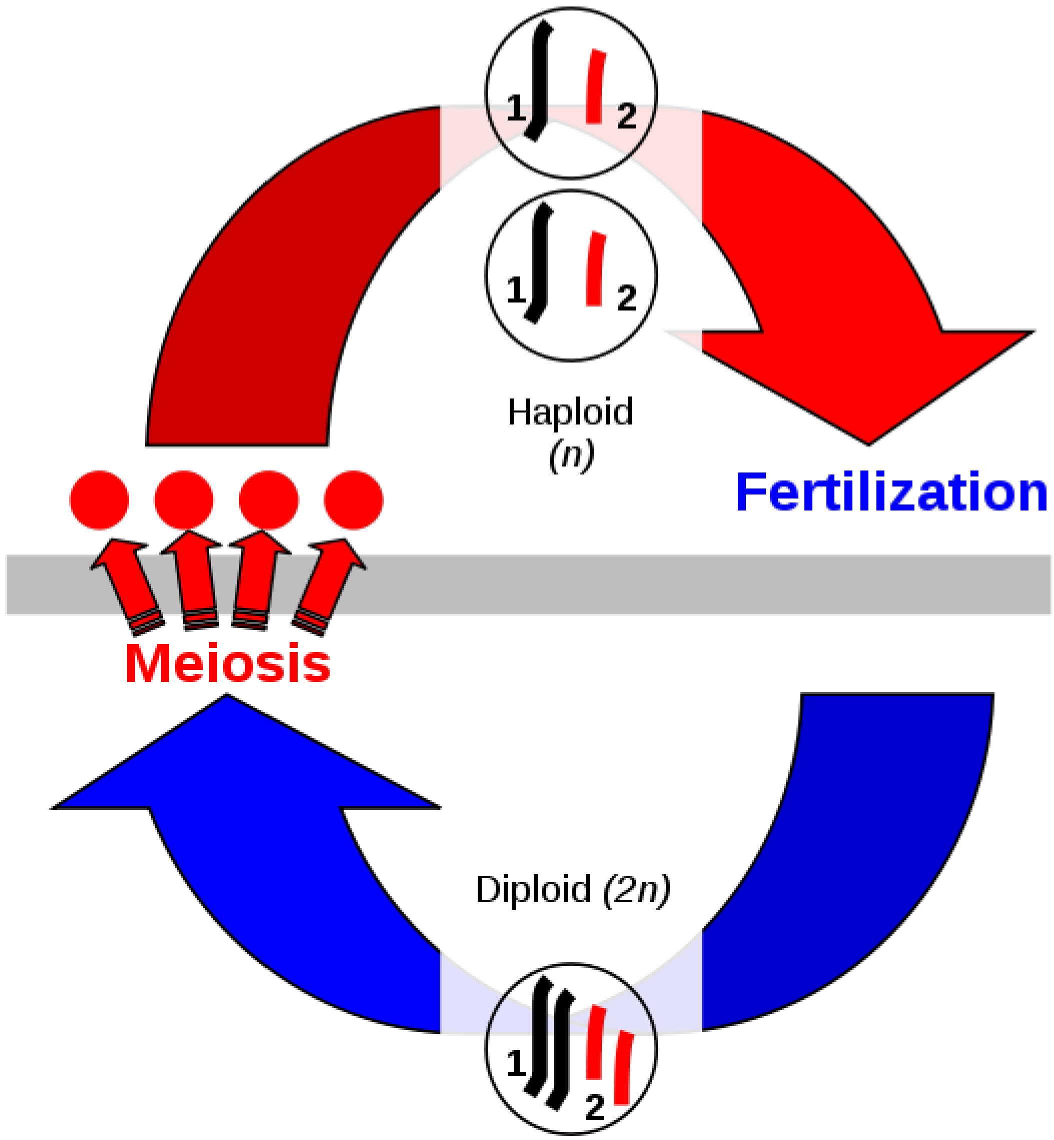
Sexual reproduction is a process specific to eukaryotes, organisms whose cells contain a nucleus and mitochondria. In addition to animals, plants, and fungi, other eukaryotes (e.g. the malaria parasite) also engage in sexual reproduction. Some bacteria use conjugation to transfer genetic material between cells; while not the same as sexual reproduction, this also results in the mixture of genetic traits.

What is considered defining of sexual reproduction is the difference between the gametes and the binary nature of fertilization. Multiplicity of gamete types within a species would still be considered a form of sexual reproduction. However, no third gamete is known in multicellular animals.

While the evolution of sex itself dates to the eukaryote stage, the origin of chromosomal sex determination is younger. The ZW sex-determination system is shared by birds, some fish and some crustaceans. Most mammals, but also some insects (*Drosophila*) and plants (*Ginkgo*) use XY sex-determination. X0 sex-determination is found in certain insects.

No genes are shared between the avian ZW and mammal XY chromosomes, and from a comparison between chicken and human, the Z chromosome appeared similar to the autosomal chromosome 9 in human, rather than X or Y, suggesting that the ZW and XY sex determination systems do not share an origin, but that the sex chromosomes are derived from autosomal chromosomes of the common ancestor of birds and mammals. A paper from 2004 compared the chicken Z chromosome with platypus X chromosomes and suggested that the two systems are related.

Sexual reproduction



The life cycle of sexually reproducing organisms cycles through haploid and diploid stages.

Sexual reproduction is a process where organisms form offspring that combine genetic traits from both parents. Chromosomes are passed on from one generation to the next in this process. Each cell in the offspring has half the chromosomes of the mother and half of the father. Genetic traits are contained within the deoxyribonucleic acid (DNA) of chromosomes — by combining one of each type of chromosomes from each parent, an organism is formed containing a doubled set of chromosomes. This double-chromosome stage is called "diploid", while the single-chromosome stage is "haploid". Diploid organisms can, in turn, form haploid cells (gametes) that randomly contain one of each of the chromosome pairs, via a process called meiosis. Meiosis also involves a stage of chromosomal crossover, in which regions of DNA are exchanged between matched types of chromosomes, to form a new pair of mixed chromosomes. Crossing over and fertilization (the recombining of single sets of chromosomes to make a new diploid) result in the new organism containing a different set of genetic traits from either parent.

In many organisms, the haploid stage has been reduced to just gametes specialized to recombine and form a new diploid organism; in others, the gametes are capable of undergoing cell division to produce multicellular haploid organisms. In either case, gametes may be externally similar, particularly in size (isogamy), or may have evolved an asymmetry such that the gametes are different in size and other aspects (anisogamy). By convention, the larger gamete (called an ovum, or egg cell) is considered female, while the smaller gamete (called a spermatozoon, or sperm cell) is considered male. An individual that produces exclusively large gametes is female, and one that produces exclusively small gametes is male. An individual that produces both types of gametes is a hermaphrodite; in some cases hermaphrodites are able to self-fertilize and produce offspring on their own, without a second organism.

Animals

Hoverflies engaging in sexual intercourse

Most sexually reproducing animals spend their lives as diploid organisms, with the haploid stage reduced to single cell gametes. The gametes of animals have male and female forms—spermatozoa and egg cells. These gametes combine to form embryos which develop into a new organism.

The male gamete, a spermatozoon (produced within a testicle), is a small cell containing a single long flagellum which propels it. Spermatozoa are extremely reduced cells, lacking many cellular components that would be necessary for embryonic development. They are specialized for motility, seeking out an egg cell and fusing with it in a process called fertilization.

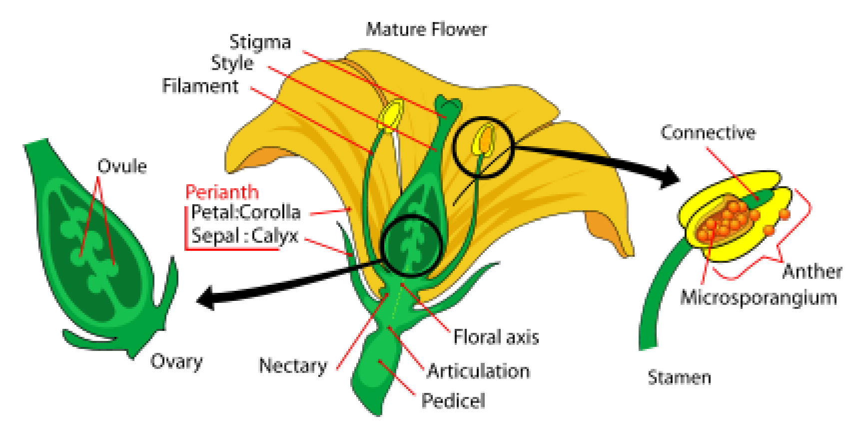
Female gametes are egg cells (produced within ovaries), large immobile cells that contain the nutrients and cellular components necessary for a developing embryo. Egg cells are often associated with other cells which support the development of the embryo, forming an egg. In mammals, the fertilized embryo instead develops within the female, receiving nutrition directly from its mother.

Animals are usually mobile and seek out a partner of the opposite sex for mating. Animals which live in the water can mate using external fertilization, where the eggs and sperm are released into and combine within the surrounding water. Most animals that live outside of water, however, must transfer sperm from male to female to achieve internal fertilization.

In most birds, both excretion and reproduction is done through a single posterior opening, called the cloaca—male and female birds touch cloaca to transfer sperm, a process called "cloacal kissing". In many other terrestrial animals, males use specialized sex organs to assist the transport of sperm—these male sex organs are called intromittent organs. In humans and other mammals this male organ is the penis, which enters the female reproductive tract (called the vagina) to achieve insemination—a process called sexual intercourse. The penis contains a tube through which semen (a fluid containing sperm) travels. In female mammals the vagina connects with the uterus, an organ which directly supports the development of a fertilized embryo within (a process called gestation).

Because of their motility, animal sexual behavior can involve coercive sex. Traumatic insemination, for example, is used by some insect species to inseminate females through a wound in the abdominal cavity – a process detrimental to the female's health.

Plants



Flowers are the sexual organs of flowering plants, usually containing both male and female parts.

Like animals, plants have developed specialized male and female gametes. Within most familiar plants, male gametes are contained within hard coats, forming pollen. The female gametes of plants are contained within ovules; once fertilized by pollen these form seeds which, like eggs, contain the nutrients necessary for the development of the embryonic plant.

Female (left) and male (right) cones are the sex organs of pines and other conifers.

Many plants have flowers and these are the sexual organs of those plants. Flowers are usually hermaphroditic, producing both male and female gametes. The female parts, in the center of a flower, are the carpels—one or more of these may be merged to form a single pistil. Within carpels are ovules which develop into seeds after fertilization. The male parts of the flower are the stamens: these long filamentous organs are arranged between the pistil and the petals and produce pollen at their tips. When a pollen grain lands upon the top of a carpel, the tissues of the plant react to transport the grain down into the carpel to merge with an ovule, eventually forming seeds.

In pines and other conifers the sex organs are conifer cones and have male and female forms. The more familiar female cones are typically more durable, containing ovules within them. Male cones are smaller and produce pollen which is transported by wind to land in female cones. As with flowers, seeds form within the female cone after pollination.

Because plants are immobile, they depend upon passive methods for transporting pollen grains to other plants. Many plants, including conifers and grasses, produce lightweight pollen which is carried by wind to neighboring plants. Other plants have heavier, sticky pollen that is specialized for transportation by insects. The plants attract these insects with nectar-containing flowers. Insects transport the pollen as they move to other flowers, which also contain female reproductive organs, resulting in pollination.

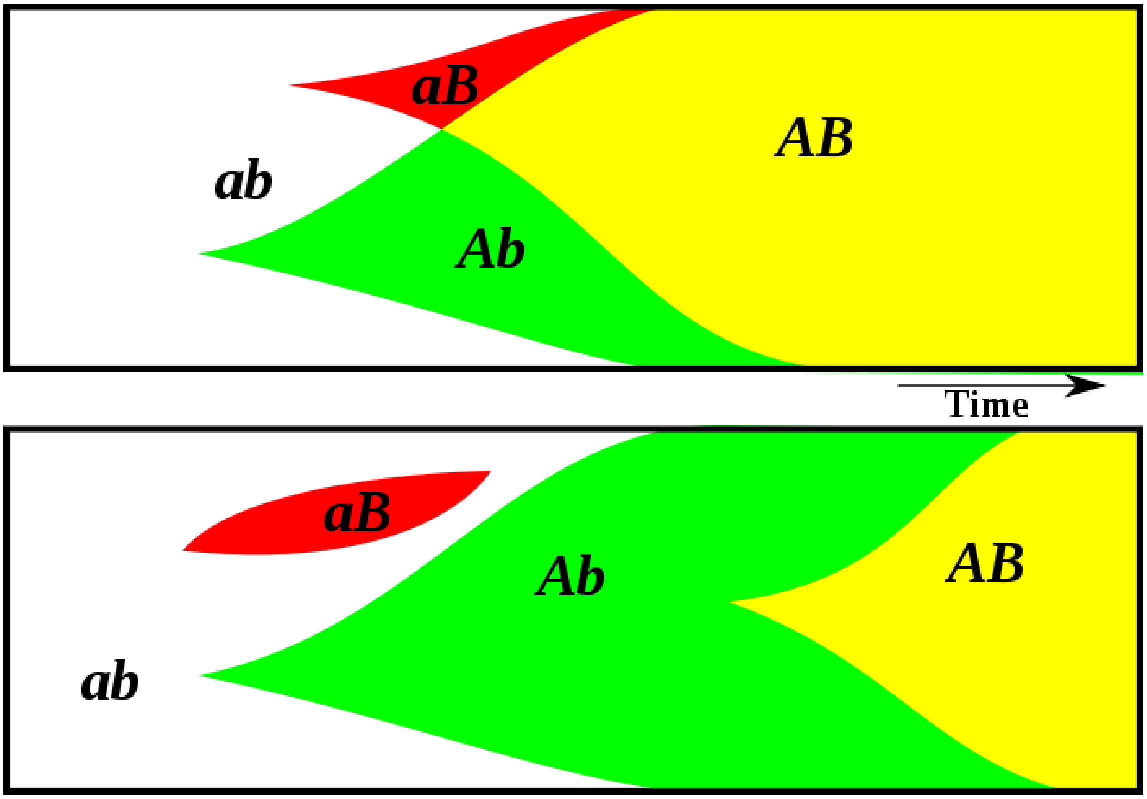
Mushrooms are produced as part of fungal sexual reproduction.

Fungi

Most fungi reproduce sexually, having both a haploid and diploid stage in their life cycles. These fungi are typically isogamous, lacking male and female specialization: haploid fungi grow into contact with each other and then fuse their cells. In some of these cases the fusion is asymmetric, and the cell which donates only a nucleus (and not accompanying cellular material) could arguably be considered "male".

Some fungi, including baker's yeast, have mating types that create a duality similar to male and female roles. Yeast with the same mating type will not fuse with each other to form diploid cells, only with yeast carrying the other mating type.

Fungi produce mushrooms as part of their sexual reproduction. Within the mushroom diploid cells are formed, later dividing into haploid spores—the height of the mushroom aids the dispersal of these sexually produced offspring.



Sex helps the spread of advantageous traits through recombination. The diagrams compare evolution of allele frequency in a sexual population (a) and an asexual population (b). The vertical axis shows frequency and the horizontal axis shows time. The alleles a/A and b/B occur at random. The advantageous combination AB arises rapidly with recombination (a), but must arise independently in (b).

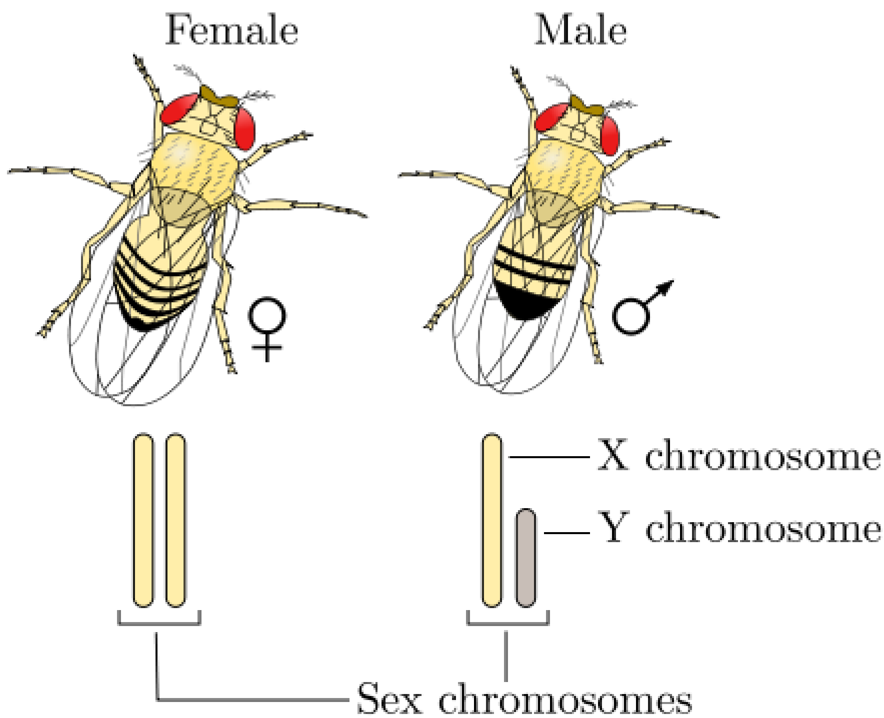
Sex determination

The most basic sexual system is one in which all organisms are hermaphrodites, producing both male and female gametes—this is true of some animals (e.g. snails) and the majority of flowering plants. In many cases, however, specialization of sex has evolved such that some organisms produce only male or only female gametes. The biological cause for an organism developing into one sex or the other is called sex determination.

In the majority of species with sex specialization organisms are either male (producing only male gametes) or female (producing only female gametes). Exceptions are common—for example, in the roundworm *C. elegans* the two sexes are hermaphrodite and male (a system called androdioecy).

Sometimes an organism's development is intermediate between male and female, a condition called intersex. Sometimes intersex individuals are called "hermaphrodite"; but, unlike biological hermaphrodites, intersex individuals are unusual cases and are not typically fertile in both male and female aspects.

Genetic



Like humans and other mammals, the common fruit fly has an XY sex determination system.

In genetic sex determination systems, an organism's sex is determined by the genome it inherits. Genetic sex determination usually depends on asymmetrically inherited sex chromosomes which carry genetic features that influence development; sex may be determined either by the presence of a sex chromosome or by how many the organism has. Genetic sex determination, because it is determined by chromosome assortment, usually results in a 1:1 ratio of male and female offspring.

Humans and other mammals have an XY sex determination system: the Y chromosome carries factors responsible for triggering male development. The default sex, in the absence of a Y chromosome, is female. Thus, XX mammals are female and XY are male. XY sex determination is found in other organisms, including the common fruit fly and some plants. In some cases, including in the fruit fly, it is the number of X chromosomes that determines sex rather than the presence of a Y chromosome (see below).

In birds, which have a ZW sex-determination system, the opposite is true: the W chromosome carries factors responsible for female development, and default development is male. In this case ZZ individuals are male and ZW are female. The majority of butterflies and moths also have a ZW sex-determination system. In both XY and ZW sex determination systems, the sex chromosome carrying the critical factors is often significantly smaller, carrying little more than the genes necessary for triggering the development of a given sex.

Many insects use a sex determination system based on the number of sex chromosomes. This is called XX/XO sex determination—the O indicates the absence of the sex chromosome. All other chromosomes in these organisms are diploid, but organisms may inherit one or two X chromosomes. In field crickets, for example, insects with a single X chromosome develop as male, while those with two develop as female. In the nematode *C. elegans* most worms are self-fertilizing XX hermaphrodites, but occasionally abnormalities in chromosome inheritance regularly give rise to individuals with only one X chromosome—these XO individuals are fertile males (and half their offspring are male).

Other insects, including honey bees and ants, use a haplodiploid sex-determination system. In this case diploid individuals are generally female, and haploid individuals (which develop from unfertilized eggs) are male. This sex-determination system results in highly biased sex ratios, as the sex of offspring is determined by fertilization rather than the assortment of chromosomes during meiosis.

Clownfish are initially male; the largest fish in a group becomes female.

Nongenetic

For many species sex is not determined by inherited traits, but instead by environmental factors experienced during development or later in life. Many reptiles have temperature-dependent sex determination: the temperature embryos experience during their development determines the sex of the organism. In some turtles, for example, males are produced at lower incubation temperatures than females; this difference in critical temperatures can be as little as 1–2°C.

Many fish change sex over the course of their lifespan, a phenomenon called sequential hermaphroditism. In clownfish, smaller fish are male, and the dominant and largest fish in a group becomes female. In many wrasses the opposite is true—most fish are initially female and become male when they reach a certain size. Sequential hermaphrodites may produce both types of gametes over the course of their lifetime, but at any given point they are either female or male.

In some ferns the default sex is hermaphrodite, but ferns which grow in soil that has previously supported hermaphrodites are influenced by residual hormones to instead develop as male.

Sexual dimorphism

Common pheasants are sexually dimorphic in both size and appearance.

Many animals have differences between the male and female sexes in size and appearance, a phenomenon called sexual dimorphism. Sexual dimorphisms are often associated with sexual selection – the competition between individuals of one sex to mate with the opposite sex. Antlers in male deer, for example, are used in combat between males to win reproductive access to female deer. In many cases the male of a species is larger in size; in mammals species with high sexual size dimorphism tend to have highly polygynous mating systems—presumably due to selection for success in competition with other males.

Other animals, including most insects and many fish, have larger females. This may be associated with the cost of producing egg cells, which requires more nutrition than producing sperm—larger females are able to produce more eggs. Occasionally this dimorphism is extreme, with males reduced to living as parasites dependent on the female.

In birds, males often have a more colourful appearance and may have features (like the long tail of male peacocks) that would seem to put the organism at a disadvantage (e.g. bright colors would seem to make a bird more visible to predators). One proposed explanation for this is the handicap principle. This hypothesis says that, by demonstrating he can survive with such handicaps, the male is advertising his genetic fitness to females—traits that will benefit daughters as well, who will not be encumbered with such handicaps.

Sex differences in humans include, generally, a larger size and more body hair in men; women have breasts, wider hips, and a higher body fat percentage.