**Reproductive behaviour,** any [activity](https://www.britannica.com/topic/mating) directed toward perpetuation of a species. The enormous range of animal reproductive modes is matched by the variety of reproductive behaviour.

Reproductive behaviour in animals includes all the events and actions that are directly involved in the process by which an organism generates at least one replacement of itself. In an [evolutionary](https://www.britannica.com/science/evolution-scientific-theory) sense, the goal of an individual in reproduction is not to perpetuate the population or the species; rather, relative to the other members of its population, it is to maximize the representation of its own genetic characteristics in the next generation. The dominant form of reproductive behaviour for achieving this purpose is sexual rather than asexual, although it is easier mechanically for an organism simply to divide into two or more individuals. Even many of the organisms that do exactly this—and they are not all the so-called primitive forms—every so often intersperse their normal asexual pattern with sexual reproduction.

**Basic concepts and features**

**The dominance of** **sexual reproduction**

Two explanations have been given for the dominance of sexual reproduction. Both are related to the fact that the [environment](https://www.merriam-webster.com/dictionary/environment) in which an organism lives changes in location and through time; the evolutionary success of the organism is determined by how well it adapts to such changes. The physiological and morphological aspects of an organism that interact with the environment are governed by the organism’s germ plasm—the genetic materials that determine [hereditary](https://www.britannica.com/science/heredity-genetics) characteristics. Unlike asexual methods, sexual reproduction allows the reshuffling of the genetic material, both within and between individuals of one generation, resulting in the potential for an extraordinary array of offspring, each with a genetic makeup different from that of its parents.

According to proponents of the so-called long-term theory for the dominance of sexual reproduction, sexual reproduction will replace asexual reproduction in the evolutionary development of an organism because it assures greater genetic variability, which is necessary if the species is to keep pace with its changing environment. According to proponents of the short-term theory, however, the above argument implies that [natural selection](https://www.britannica.com/science/natural-selection) acts on groups of organisms rather than on individuals, which is contrary to the Darwinian concept of natural selection (see [evolution: The concept of natural selection](https://www.britannica.com/science/evolution-scientific-theory/The-science-of-evolution#toc49853)). They prefer to view the advantages of sexual reproduction on a more immediate and individual level: an organism employing sexual reproduction has an advantage over one employing asexual means because the greater variety of offspring produced by the former results in a larger number of genes being transmitted to the next generation. The latter view is probably more nearly correct, especially in violently fluctuating and unpredictable [environments](https://www.merriam-webster.com/dictionary/environments). The former theory is probably correct when viewed in terms of its advantage to individuals that are spreading in geographic range, thereby increasing the likelihood of encountering different environments

**Natural selection and reproductive behaviour**

Natural selection places a premium on the evolution of those physiological, morphological, and behavioral [adaptations](https://www.merriam-webster.com/dictionary/adaptations) that will increase the [efficiency](https://www.merriam-webster.com/dictionary/efficiency) of the exchange of genetic materials between individuals. Organisms will also evolve mechanisms for sensing whether or not the environment is always permissive for reproduction or if some times are better than others. This involves not only the evolution of environmental sensors but also the [concurrent](https://www.merriam-webster.com/dictionary/concurrent) evolution of mechanisms by which this information can be processed and acted upon. Because all seasons are not usually equally [conducive](https://www.merriam-webster.com/dictionary/conducive), individuals whose genetic backgrounds result in their reproducing at a more favourable rather than less favourable [period](https://www.britannica.com/science/biological-periodicity) will eventually dominate succeeding generations. This is the basis for the seasonality of reproduction among most animal species.

Natural selection also results in the evolution of systems for transmitting and receiving information that will increase the efficiency of two individuals’ finding each other. These attraction systems are usually, but not always, [species](https://www.britannica.com/science/species-taxon) specific (see [evolution: Species and speciation](https://www.britannica.com/science/evolution-scientific-theory/The-science-of-evolution)). Once the proper individuals have found each other, it is clearly important that they are both in a state of reproductive readiness. That their sensory receptors are tuned to the same environmental stimuli is usually sufficient to achieve this synchrony (proper timing) in the lower organisms. Apparently, however, this is not enough in the more complex organisms, in which the fine tuning for reproductive synchrony is accomplished chiefly by a process called [courtship](https://www.britannica.com/topic/courtship). Another evolutionary necessity is a mechanism that will guide the partners into the proper orientation for efficient copulation. Such mechanisms are necessary for both internal and external [fertilization](https://www.britannica.com/science/fertilization-reproduction), especially the latter, where improper orientation could result in a complete waste of the eggs and sperm

In most organisms, the period of greatest mortality occurs between birth or hatching and the attainment of maturity. Thus, it is not surprising that some of the most elaborate evolutionary adaptations of an organism are revealed during this period. Natural selection has favoured an enormous variety of behaviour in both parents and offspring that serves to ensure the maximum survival of the young to maturity. In some animals this involves not only protecting the young against environmental [vicissitudes](https://www.merriam-webster.com/dictionary/vicissitudes) and providing them with adequate nutrition but also giving them, in a more or less active manner, the information they will need to reproduce in turn.

External and internal influences

As mentioned at the beginning of this discussion, the anatomical, physiological, and neurological aspects of reproduction and behaviour are dealt with in other articles. It is useful here, however, to consider briefly the external and internal factors that initiate reproductive behaviour.

## Environmental influences

[Light](https://www.britannica.com/science/photoperiodism), usually in the form of increasing day length, seems to be the major environmental stimulus for most vertebrates and many invertebrates, especially those living in areas away from the Equator. That this should be such an important factor is quite reasonable in an evolutionary sense: increasing day length signifies the onset of a favourable period for reproduction. In equatorial regions, where changes in day length are usually insignificant throughout the year, other environmental stimuli, such as rain, predominate.

Superimposed on day length are usually several other factors, which, if lacking, often override the stimulating effect of light. Many insects, for example, will not initiate a reproductive cycle if they lack certain protein foods. Many animal groups have an internal cycle of cellular activity that must coincide with the external factors before reproduction can occur; a familiar example is the [estrous](https://www.britannica.com/science/estrus) cycle in most mammals except primates. Females are sexually receptive only during a brief period when they have ovulated (released an egg from the ovary).

**Hormonal Influence**

Although the exact way by which light affects the reproductive cycle is still disputed, it undoubtedly varies from group to group. In birds, light passes either through the eyes or through the bony tissue of the skull and stimulates the development of certain cells in the forepart of the brain. These cells then secrete a substance that stimulates the anterior [pituitary gland](https://www.britannica.com/science/pituitary-gland), which is located at the base of the brain, to produce an array of regulatory substances ([hormones](https://www.britannica.com/science/sex-hormone)), called [gonadotropins](https://www.britannica.com/science/gonadotropin), that are carried by the blood to the [gonads](https://www.britannica.com/science/gonad) (ovaries and testes), where they directly stimulate the development of eggs and sperm. The gonads, in turn, produce the sex hormones—[estrogen](https://www.britannica.com/science/estrogen) in the female and [testosterone](https://www.britannica.com/science/testosterone) in the male—that directly control several overt aspects of reproductive behaviour.

Unlike the higher animals, the gonads of [insects](https://www.britannica.com/animal/insect) apparently do not themselves secrete hormones. Instead, stimulation by the [corpus allatum](https://www.britannica.com/science/corpus-allatum), an organ in insects that corresponds in function to the pituitary gland, causes the secretion of liquid substances on the body surface. These substances are transmitted as liquids, or, even more significantly, as gases, to the recipient, in which they are usually detected by olfaction or taste. Such substances, which are called ectohormones, or [pheromones](https://www.britannica.com/science/pheromone), may serve as the major regulation and [communication](https://www.britannica.com/topic/communication) system for reproduction as well as other behaviour in insects.

In the absence of all other stimuli, many types of sexual behaviour can be induced simply by an injection of the appropriate gonadal hormone. Conversely, removal of the gonads usually [inhibits](https://www.merriam-webster.com/dictionary/inhibits) most sexual behaviour. The apparent failure of complete hormonal control over reproductive behaviour has been a subject of much investigation and dispute. There is much evidence that many types of reproductive behaviour are or can be controlled solely by neural mechanisms, bypassing the hormonal system and any effect that it might exert on the [nervous system](https://www.britannica.com/science/nervous-system) to produce behaviour. Several types of reproductive behaviour controlled solely or almost solely by neural mechanisms are involved in or triggered by the processes that are initiated by [courtship](https://www.britannica.com/topic/courtship).

Modes of Sexual reproduction

The chief [clues](https://www.britannica.com/science/senses) by which [organisms advertise](https://www.britannica.com/topic/animal-communication) their readiness to engage in reproductive activity are visual, auditory, and olfactory in nature. Most animals use a combination of two modes; sometimes all three are used.

## Visual clues

The appearance of many higher vertebrates changes with the onset of reproductive activity. The so-called prenuptial [molt](https://www.britannica.com/science/molt) in many male birds results in the attainment of the nuptial plumage, which often differs radically from that possessed by the bird at other times of the year or from that possessed by a nonreproductive individual. The hindquarters of female [baboons](https://www.britannica.com/animal/baboon) become bright red in [colour](https://www.britannica.com/science/coloration-biology), which indicates, or advertises, the fact that she is in estrus and sexually receptive. Such changes in appearance are less common in the lower animals but do occur in many fishes, crabs, and cephalopods (e.g., squids and octopuses).

Often associated with changes in appearance are changes in behaviour, particularly the increase in [aggressive behaviour](https://www.britannica.com/topic/aggressive-behaviour) between males, often a prime feature in attracting females; such changes have interesting evolutionary [implications](https://www.merriam-webster.com/dictionary/implications). In certain [grouse](https://www.britannica.com/animal/grouse), for example, females are most attracted to males that engage in the greatest amount of fighting. No doubt, fighting in some groups of mammals also serves this function as well as others.

In many animals the rise in aggression takes the form of [territoriality](https://www.britannica.com/topic/territorial-behaviour), in which an individual, usually a male, defends a particular location or territory by excluding from it all other males of his own kind. Occasionally, other species are also excluded when it is to the advantage of the defending individual to do so. Territorial behaviour involves many functions, not all of which are directly concerned with reproduction. For purposes of advertising, however, territoriality probably reduces the amount of [interference](https://www.britannica.com/topic/inhibition-psychology) between males and also makes it easier for females to find males at the proper time

Auditory clues

The fact that [sound](https://www.britannica.com/topic/sound-production) signals can travel around barriers, whereas visual signals cannot, accounts for their widespread use in indicating sexual receptiveness, especially in [frogs](https://www.britannica.com/animal/frog), insects, and birds. Like visual signals, a sound for advertising purposes usually encodes several pieces of information; for example, the signals usually reveal to the receiver the caller’s species, its sex, and, in some cases, whether or not it is mated. The [vocalizations](https://www.britannica.com/topic/vocalization) of one type of frog also reveal the number of other males located nearby. This information, a critical clue for females, is a measure of how good the habitat is for depositing eggs. The sounds produced by the wings of [mosquitoes](https://www.britannica.com/animal/mosquito-insect) attract females and are species specific. Humans have taken advantage of this signal by using artificial sound generators to [eradicate](https://www.merriam-webster.com/dictionary/eradicate) certain mosquitoes. Advertising signals also serve to repel other males; a classical example is the territorial song of many [songbirds](https://www.britannica.com/animal/songbird).

## Olfactory clues

Researchers have now become aware of the enormous amount of information that is passed between animals by chemical means. Well known are the [urine](https://www.britannica.com/science/urine), feces, and scent markings employed by most mammals to delimit their breeding territories and to advertise their sexual state. Males of a number of mammals are capable of determining if a female will be sexually receptive simply by smelling her urine markings. A substance in the urine of male [mice](https://www.britannica.com/animal/mouse-rodent), on the other hand, actually induces and accelerates the estrous cycle of females. A female [gypsy moth](https://www.britannica.com/animal/gypsy-moth) is able to attract males thousands of metres downwind of it simply by releasing minute quantities of its sex pheromone each second. It has been calculated that one female [silkworm moth](https://www.britannica.com/animal/silkworm-moth) carries only about 1.5 micrograms (1.5 × 10-6 gram) of its sex attractant, called bombykol, at any given moment; theoretically, this is enough to activate more than 1,000,000,000 males. The sex attractant of [barnacles](https://www.britannica.com/animal/barnacle), which are otherwise rather sessile (sedentary) organisms, causes individuals to [aggregate](https://www.merriam-webster.com/dictionary/aggregate) during the breeding period

Another possible channel of communication occurs in a few fishes, namely [electric](https://www.britannica.com/science/bioelectricity) discharge. Evidence suggests that weak electric fields and discharges in the [Mormyridae](https://www.britannica.com/animal/mormyrid) of Africa and [Gymnotidae](https://www.britannica.com/animal/knifefish) of [South America](https://www.britannica.com/place/South-America) represent the major mode of social interaction in these families

## Courtship

Synchrony is the major factor in achieving fertilization in the lower animals, particularly in aquatic forms. In most of these groups, the eggs and sperm are simply discharged into the surrounding water, and fertilization occurs externally. It might be assumed that this procedure would be roughly the same in the higher animals, with perhaps more overt behaviour to achieve synchrony, and that, after the two individuals found each other, fertilization would proceed fairly quickly. This is usually not the case, however. Although fertilization in the higher terrestrial forms involves contact during [copulation](https://www.britannica.com/science/sexual-intercourse), it has been suggested that all of the higher animals may have a strong [aversion](https://www.merriam-webster.com/dictionary/aversion) to bodily contact. This aversion is no doubt an antipredator mechanism: close bodily contact signifies being caught. Since females are in an especially helpless situation during copulation, they are particularly wary about bodily contact. In addition, males are particularly aggressive during the breeding period, which further increases the uncertainty of both individuals. These difficulties were solved by the evolution of a collection of behaviours called courtship. Courtship has been defined as the heterosexual reproductive communication system leading to the consummatory sexual act.

Courtship behaviour has many advantages and functions, including the reduction of hostility between the potential sex partners, especially in species in which the male actively defends a territory. The major aspects of such behaviour seem to be appearance, persistence, appeasement, [persuasion](https://www.britannica.com/topic/persuasion-psychology), and even deception. Because courtship behaviour involves the transmission of information by means of signals, it is useful to define at this point an important group of social signals called [displays](https://www.britannica.com/topic/display-behaviour).

A social signal may be considered any behavioral pattern that effectively conveys information from one individual to another. The term display has been restricted by some authorities to social signals that not only convey information but that, in the course of evolution, have also become “ritualized.” In other words, such signals have become so specialized and exaggerated in form or function that they expressly [facilitate](https://www.merriam-webster.com/dictionary/facilitate) a certain type of communication. The visual, auditory, olfactory, [tactile](https://www.merriam-webster.com/dictionary/tactile), or other patterns by which organisms advertise their readiness to engage in reproductive activity provide examples of displays. Clearly, the kinds of displays utilized by organisms depend on the sensory receptors of the receiver. Whereas higher vertebrates tend to use visual and auditory displays, insects tend toward olfactory and tactile displays.

In animals in which the male takes on a wholly [different appearance](https://www.britannica.com/science/sexual-dimorphism) during the breeding period, natural selection has eliminated from the female’s appearance the “aggressive badges” of males that provoke fighting. It is not without significance that the appearance of the adult female in many species is much like that of the juvenile; this implies to the male a friendly, nonaggressive relationship. When one male approaches another that has intruded into the former’s [territory](https://www.britannica.com/topic/territorial-behaviour), the outsider may either return the aggressive display or flee. Females, however, usually quietly back up slightly and then slowly move forward again. With each approach, the male’s hostility lessens toward this appeasing, increasingly familiar individual. Often, as in many birds, the females resort to displays that resemble the food-begging behaviour normally seen in the young. Males frequently respond to this display by actually regurgitating food. Male [spiders](https://www.britannica.com/animal/spider-arachnid) of some species offer the larger and more aggressive females food as bait, and copulation occurs while the female is eating the food rather than her potential mate. Mutual feeding displays, often with nonedible items, are engaged in by a number of insects and birds. In the courtship behaviour of several birds, extremely elaborate displays are utilized to hide the bill from the potential partner, because the bills of these birds are their chief weapons. Some aspects of nest building have been incorporated into the displays of such birds as [penguins](https://www.britannica.com/animal/penguin). Early in the relationship between the individuals, one or both may offer the other stones that are placed in a pile. The actual nest is not constructed until much later, however.

All courtship displays resemble functional behaviours that are appropriate to friendly, bonded situations, such as those between parents and between parents and their offspring. The degree of elaborateness of the display is governed by a number of factors. One is to prevent cross-mating between different [species](https://www.britannica.com/science/species-taxon), an occurrence that usually results in the waste of the eggs and sperm. Any specific aspect—i.e., one or more displays—used by an organism in species [discrimination](https://www.merriam-webster.com/dictionary/discrimination) is called an isolating mechanism. In many species, the majority of the displays between individuals are a series of identity checks.

Another factor that has an impact upon the complexity of displays is the length of time that the [pair bond](https://www.britannica.com/topic/pair-bonding) will endure. Brief relationships are usually, but not always, associated with rather simple courtship activity. In a number of insects, birds, and mammals, the males display on a common courtship ground called a [lek](https://www.britannica.com/topic/lek) or an arena. Females visit these courtship areas, copulate, and leave. The males do not participate in any aspect of parental care; the bond lasts but a few seconds. Yet, despite the [brevity](https://www.merriam-webster.com/dictionary/brevity) of this relationship, in no other courtship system is there the development of such elaborate and almost fantastic displays in both the movements and appearances of the courting males.

**Post-fertilization behaviour**

Various types of behaviour ensure that a maximum number of [fertilized](https://www.britannica.com/science/fertilization-reproduction) eggs or young will survive to become reproductive adults. Clearly, the number of eggs produced and their size represents a balance achieved by natural selection. This balance conforms to some optimum compromise between producing many eggs containing little food for the development of young or fewer eggs with more provisions.

There has been considerable controversy about the factors that limit the number of offspring an organism can produce. It has been suggested that, among animals in which the offspring are dependent on the parents for varying lengths of time, clutch or litter size has been adjusted through natural selection to the maximum number of offspring that the parents, on the average, can feed. There are, on the other hand, organisms that do not practice parental care and produce millions of eggs. According to one school of [thought](https://www.britannica.com/topic/thought), these species have such a high fecundity (productivity) because the eggs and larvae suffer a very high [mortality](https://www.britannica.com/science/mortality-demography) rate. Hence, it is necessary for such animals to produce thousands, even millions, of eggs just to obtain a few reproductive adults. An opposing school of thought, however, says that such species have high mortality rates because of their great fecundities. By similar [reasoning](https://www.britannica.com/topic/reason), low death rates would be the consequence of low fecundity.

**Protective** **adaptations**

A number of adaptations have evolved to protect the [eggs](https://www.britannica.com/science/egg-biology) and [larvae](https://www.britannica.com/science/larva) of species not attended by adults. In one such [adaptation](https://www.merriam-webster.com/dictionary/adaptation), the eggs or larvae are distasteful, inedible, or apparently harmful to potential enemies. The eggs of the jellyfish *Bougainvillia*, for example, contain stinging cells on the surface that deter predators. Many female [butterflies](https://www.britannica.com/animal/butterfly-insect) deposit their eggs on plants that contain poisonous [compounds](https://www.merriam-webster.com/dictionary/compounds), which the larvae incorporate into their bodies, making them distasteful. When disturbed many insect larvae, especially those that are camouflaged, give a so-called startle display; several [caterpillars](https://www.britannica.com/science/caterpillar), for example, raise their heads as if to bite or their hindparts, in the manner of a wasp, as if to sting. Others suddenly present striking colour patterns previously hidden. Most of these displays have been shown experimentally to be effective deterrents against predators.

**Caring for offspring**

Animals that do not care for their young must provide for the nutritional needs of their offspring. One way of doing so is by producing an egg with a sufficiently large [yolk](https://www.britannica.com/science/yolk) supply that the young, when hatched, are already at an advanced, almost independent state. A peculiar example of this is found in the [incubator birds](https://www.britannica.com/animal/megapode) (Megapodiidae), which cover their large eggs with soil and debris to create a mound of considerable depth, effectively providing heat for the developing eggs. After a very long incubation period, the young emerge as fully feathered miniature adults and are capable of flying in 24 hours. Before sealing the nest that they make for their eggs, many insects, such as certain solitary [wasps](https://www.britannica.com/animal/wasp), stock the nest with food. In a more bizarre manner, other solitary wasps place one egg in the body of an insect or spider previously paralyzed by the wasp. Upon hatching, the larva eats the still living host.

Social [parasitism](https://www.britannica.com/science/parasitism), another fascinating aspect of post-fertilization behaviour, is found in certain insects and birds. In this case, the true parents do not care for their eggs or offspring; rather, they place them under the foster care of other species, often, but not always, to the detriment of the foster parents’ offspring. In certain parasitic species of [cuckoos](https://www.britannica.com/animal/cuckoo), the females are divided into groups, or gentes, each of which lays eggs with a colour and pattern unlike those of the other groups. The females of each group usually select a particular species as the host, and, more often than not, the eggs of the parasite closely resemble those of the potential foster parent. This [mimicry](https://www.britannica.com/science/mimicry) has evolved because many host species throw eggs not resembling their own out of the nest. Some young cuckoos also exhibit a behaviour called backing, in which they push out the other nestlings and monopolize the food supply.

**Parental care**

Among the organisms that remain with the eggs or offspring, one particular behaviour is striking—that of nest construction to keep the eggs and larvae in one spot and to protect them against predators as well as such environmental factors as sun and rain. The placement of a nest usually serves an antipredatory purpose, as in birds that put their nests near those of social wasps or stinging ants. Although they are not normally thought to do so, many mammals, particularly rodents and carnivores, construct special nests, dens, or burrows solely for reproductive purposes.

A number of fishes build nests made of bubbles that not only hold the eggs together but also provide the oxygen necessary for the developing embryos. Other fishes, particularly those that live in oxygen-poor waters, display elaborate fanning behaviour to keep the water moving around the eggs. In some fishes, the female incubates the egg in her mouth, thus providing protection against predators as well as constant aeration. The fry (young) of some of these [mouthbreeders](https://www.britannica.com/science/mouthbreeder) travel in a school near the parent. When danger approaches, they flee into the parent’s mouth and later swim out after the danger passes.

Birds have the problem of keeping the eggs at an optimum temperature for development of the embryo. With the onset of egg laying in many species, the feathers of the lower abdomen are lost, and the skin in that area becomes thickened and highly vascularized (filled with blood vessels), forming the so-called [brood patches](https://www.britannica.com/science/brood-patch). Usually the female develops these patches, which serve to transfer more effectively to the eggs the warmth from the adult’s body. It has been shown that, like much of parental behaviour in the higher vertebrates, brood patches and “broodiness” are controlled by several [hormones](https://www.britannica.com/science/sex-hormone), combined with visual and tactile stimuli. Chief among these hormones is [prolactin](https://www.britannica.com/science/prolactin), which also controls the production of [pigeon](https://www.britannica.com/animal/pigeon) milk, a cheeselike substance produced only in the crops of adult [doves](https://www.britannica.com/animal/dove-bird) and pigeons and fed to the nestlings by regurgitation.

Although there are some outstanding exceptions, most young [mammals](https://www.britannica.com/animal/mammal) are completely helpless at birth. This helplessness is most striking in the [marsupials](https://www.britannica.com/animal/marsupial) (*e.g.,* opossums and kangaroos), in which the young are born at a very early stage of development; they crawl through the mother’s hair to the [brood pouch](https://www.britannica.com/science/brood-pouch), where they attach themselves to a nipple and their development continues for many more months.

An early characteristic behaviour in mammals following birth is that of the mother licking the newborn. This serves at least two functions—one is general cleanliness to avoid infections or the attraction of parasites; the other would appear to be purely social. If a newborn mammal is removed from its mother and cleaned elsewhere before she can lick it, she usually will not accept it. Thus, licking behaviour also serves, in some manner, to establish a unique relationship between the mother and her offspring. Another characteristic mammalian behaviour is the [suckling](https://www.britannica.com/topic/suckling) response of the newborn. Although this behaviour has been claimed to be the perfect instinctive response, it apparently is not so in many species; the trial-and-error period during which the newborn discovers the nipple, however, is quite short.

In birds, especially those that nest on the ground, one of the first adult responses to the [hatching](https://www.britannica.com/science/hatching-biology) of the eggs is to remove the [conspicuous](https://www.merriam-webster.com/dictionary/conspicuous) eggshells from the area of the nest. It has been shown experimentally that, in gulls at least, this is an important antipredatory measure. When birds hatch, they have the ability to stretch their heads and to gape for food in response to any mechanical disturbance, such as that produced when the parent lands on the nest. Later in development, they stretch and gape only when the parents appear. This is another type of adaptive, antipredatory behaviour, as it would be dangerous for the nestlings to gape and vocalize in response to any environmental disturbance.

**Group care**

The ability of an animal to identify its own offspring at an early stage is apparently not important in animals that nest or are solitary breeders; offspring in the nest belong to that parent. In [colonially](https://www.britannica.com/topic/colony-animal-society) breeding species or in those where the offspring of different parents are likely to become mixed, however, natural selection has favoured the evolutionary development of behaviour that makes possible the recognition by the parent of its own offspring, thereby avoiding the danger of expending energy on offspring that do not possess the parent’s genes.

There is, on the other hand, the situation in which the offspring are cared for by individuals who are not the parents. This phenomenon occurs among the social insects in particular and also among several groups of birds and mammals; future investigations may show it to be even more widespread. In such birds as the [anis](https://www.britannica.com/animal/ani-bird), the effective breeding group consists of several females and males. One nest is constructed in which all the females deposit their eggs, and all individuals participate in the care of the resulting offspring. In certain [jays](https://www.britannica.com/animal/jay) (Corvidae), the offspring of one generation participate in the care of the offspring of the next or another generation, but the exact family relationships among the participants are not clear.

In the social insects, this type of parental behaviour apparently results from the peculiar genetic relationships between the individuals in most social-insect colonies (termites are among the exceptions). The female and, in the termites, both the male and the female can control by chemical means the kinds (called castes in ants and termites) and sexes of the offspring. An outstanding feature of such colonial insects as the [honeybee](https://www.britannica.com/animal/honeybee) is that the majority of the individuals produced by the queen are sterile; these are the workers, the individuals who care for and feed both the queen and her offspring, the sibs of the workers.

The queen is diploid in genetic makeup; that is to say, half of her genes are derived from her mother and half from her father. The males ([drones](https://www.britannica.com/animal/drone-bee)) are haploid; that is, they have only half the genes possessed by the queen, all of them derived from the mother. A queen produces eggs fertilized by sperm she has retained in her body from the mating flight; thus the individuals produced are diploid, but, unlike the queen, they are sterile. This sterility results indirectly from a chemical secreted by the queen, called the [queen substance](https://www.britannica.com/science/queen-substance). It inhibits the [workers](https://www.britannica.com/topic/worker) from building special brood cells that give rise to sexually developed individuals. If the queen fails to secrete this substance because of age or death, the workers immediately construct special brood cells with a substance they secrete; called [royal jelly](https://www.britannica.com/science/royal-jelly), it is necessary for the development of a larva then destined to be a queen.

How can the evolution of sterility in workers and their care of offspring not their own be accounted for? One possible explanation concerns the coefficient of relationship (the number of genes on the average shared in common) among the individuals of a colony. Because of the peculiar haplo-diploid mode of [sex determination](https://www.britannica.com/science/sex-determination), the workers (sisters) share all the genes from their father and, on the average, half of those from their mother. Since each worker receives half of its genes from the father and half from the mother, the average genes shared between any two workers (sisters) is three-fourths. But between mother (the queen) and daughter (a worker) this average is only one-half. The offspring (the sterile workers), therefore, may contribute more to their fitness (the maximum representation of their genes in the next generation) by caring for their sisters than by providing an equal amount of care to their “own” offspring, had they been fertile rather than sterile. A drone, on the other hand, has a coefficient of relationship with one of his sterile sisters of only one-fourth, but retains a relationship of one-half with his mother and daughters (future sterile workers). This explains why workers provide more care for their sisters than for their brothers, and why the workers eventually drive off the almost useless drones, which are relatively scarce (having resulted from unfertilized eggs), from the colony. Because sisters share more genes with each other than with their brothers, they maximize the chances of these genes surviving into the next generation by providing more care for their sisters.

This explanation of group care and extreme sociality does not account for all cases. Indeed, termites are perhaps the most extreme among animals in these respects but lack the haplo-diploid sex determination mechanism. In addition, several groups having this mechanism have not evolved extreme brood care and sociality. Other factors have to interact for these systems to evolve, but it is not yet clear what they are.

# Reproductive behaviour in invertebrates

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## Protozoans and sponges

Most protozoans (one-celled organisms) reproduce asexually, usually by [fission](https://www.britannica.com/science/binary-fission) (splitting in two); in some species, however, sexual as well as asexual reproduction occurs and may be complex. The colonial organism *[Volvox](https://www.britannica.com/science/Volvox)*, which may be either of one “sex” or composed of cells of both sexes, produces true eggs and sperm. A chemical substance released by “females” induces the production of sperm packets; following the union of the egg and sperm, the parent colony dissolves, and the zygote (fertilized egg) is released.

Another form of reproduction in protozoans is [conjugation](https://www.britannica.com/science/conjugation-sexual-process), in which organisms such as *[Paramecium](https://www.britannica.com/science/Paramecium)* fuse together briefly to exchange nuclear products. This results in a reshuffling of hereditary characteristics just as occurs in true sexual reproduction in higher animals. In some species of Paramecium, there are mating types, and an individual is of one type or the other. Opposite types apparently recognize each other by a chemical (pheromone) that is released on their body.

In the lower [metazoans](https://www.britannica.com/animal/Metazoa) (multicellular organisms), reproduction is also by both asexual and sexual means. As befits their sessile life-style and low population densities, [sponges](https://www.britannica.com/animal/sponge-animal) that reproduce sexually are usually [hermaphroditic](https://www.britannica.com/science/hermaphroditism); that is, each individual is capable of producing both sperm and eggs, but often at different times to prevent self-fertilization. The sperm are swept by water currents into another sponge, where they are picked up by specialized cells called [choanocytes](https://www.britannica.com/science/choanocyte) and carried to the egg. Fertilization takes place when a choanocyte fuses with the egg. The free-swimming larval stage that is produced is of short duration, after which the organism settles on the bottom and becomes a new adult sponge.

## Coelenterates

Hydroids, jellyfishes, sea anemones, and corals of the phylum Coelenterata, or [Cnidaria](https://www.britannica.com/animal/cnidarian), reproduce by a variety of mechanisms. A familiar coelenterate animal, the freshwater *[Hydra](https://www.britannica.com/animal/Hydra-hydrozoan-genus)*, usually reproduces asexually by [budding](https://www.britannica.com/science/budding-reproduction), a process by which small portions of the adult structure become new, but genetically identical, individuals. Hydras are also [dioecious](https://www.britannica.com/science/dioecism); that is, each individual produces either sperm or eggs. In many temperate-zone species of Hydra, sexual reproduction occurs during the autumn; the fertilized eggs enable the species to survive the winter.

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Most of the other hydrozoans are colonial organisms, often occurring in [polyp](https://www.britannica.com/science/polyp-zoology) and [medusal](https://www.britannica.com/science/medusa-invertebrate-body-type) (umbrella-shaped) forms. In a colony, reproductive individuals called [gonophores](https://www.britannica.com/science/gonophore) develop into free-swimming organisms (medusae) that reproduce sexually. Fertilization can be either external or internal; if external, the eggs are shed directly into the water. Internal fertilization results in larvae that swim out of the parent and soon settle on a surface, where they develop into another hydroid colony.

[Sea anemones](https://www.britannica.com/animal/sea-anemone) and the polyps of [corals](https://www.britannica.com/animal/coral) reproduce both asexually—by budding—or sexually. In the sexual mode, sea anemones have both dioecious and hermaphroditic species. One interesting aspect of sea anemones, which undergo internal [fertilization](https://www.britannica.com/science/fertilization-reproduction), is that they are among the first lower animals known to provide parental care. The larvae of sea anemones remain inside the adult until they are ready to metamorphose (change in form), at which time they swim from the parent’s mouth and settle on its base, remaining there until they develop tentacles. When they have reached this stage of development, they move away from the parent’s protection.

## Flatworms and rotifers

The reproductive structures of flatworms (phylum Platyhelminthes) resemble those found in the higher groups. Such flatworms as the land and freshwater [planarians](https://www.britannica.com/animal/planarian) are hermaphrodites. Although some species can reproduce asexually by splitting in two, most engage in copulation. Some freshwater planarians can produce both thin-shelled summer eggs, which hatch in a short time, and thick-shelled winter eggs, which are resistant to freezing and hatch in the spring. An apparently unique situation in many planarians is that nutrition for the embryo is supplied by the addition of separate cells to the zygote, after which the entire mass is enclosed in the shell; more commonly, the yolk is incorporated within the structure of the zygote itself.

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In the [rotifers](https://www.britannica.com/animal/rotifer) (phylum Aschelminthes), small but abundant freshwater animals, reproduction is usually sexual, and the sexes are separate. Copulation occurs by injection of sperm anywhere in the body wall of the female. Many species found in temporary ponds and streams exhibit a peculiar reproductive behaviour that is well adapted to their [transient](https://www.merriam-webster.com/dictionary/transient) environment: they produce different kinds of eggs at different times of the year. One egg type, called amictic, is produced in the early spring. These eggs apparently cannot be fertilized, and the embryo develops without fertilization ([parthenogenesis](https://www.britannica.com/science/parthenogenesis)); the result is females with a life-span no longer than two weeks. When the population reaches a peak in the early summer, a second type of egg is produced. If unfertilized, this egg, which is called mictic, results in males. As the male population increases, most mictic eggs become fertilized, resulting in the production of a heavy-shelled dormant egg with much yolk. The dormant egg survives the winter and gives rise to the amictic females of the next spring. Thus, despite the many generations produced in the summer by so-called sexual means, the reshuffling and recombination of genetic material occurs only once a year.

## Segmented worms

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The [marine worms](https://www.britannica.com/animal/polychaete) of the class Polychaeta (e.g., clam worms and lugworms of the phylum Annelida) provide the first examples of a kind of courtship behaviour involving both visual and chemical displays initiated by some rather subtle environmental stimuli. Most polychaetes reproduce sexually, and there are two distinct sexes in most species. Either by transformation or budding, many polychaetes produce a reproductive form ([epitoke](https://www.britannica.com/science/epitoke)). At a certain time of the year, the epitokes swarm to the ocean surface and engage in mass shedding of eggs and sperm. Some female epitokes of [clam worms](https://www.britannica.com/animal/rag-worm) (Nereis) produce a chemical substance called [fertilizin](https://www.britannica.com/science/fertilizin) that attracts the male epitokes and stimulates the shedding of sperm. Male epitokes of a polychaete found in the [Atlantic Ocean](https://www.britannica.com/place/Atlantic-Ocean) emit a flashing [light](https://www.britannica.com/science/bioluminescence); females emit a steady light. The light may serve to attract male and female and to aid in species discrimination. The swarming of the [palolo worm](https://www.britannica.com/animal/palolo-worm) Palola in parts of the South Pacific is apparently triggered by an annual and a lunar cycle; the epitokes separate from the parent (atoke) in October or November, during the last part of the [lunar cycle](https://www.britannica.com/science/Metonic-cycle).

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The class [Oligochaeta](https://www.britannica.com/animal/oligochaete) (phylum Annelida) contains a [diversity](https://www.merriam-webster.com/dictionary/diversity) of both aquatic and terrestrial worms, among which is the familiar [earthworm](https://www.britannica.com/animal/earthworm), Lumbricus. Although some aquatic oligochaetes reproduce asexually, the majority are sexual, and all of these are hermaphrodites. At mating, two oligochaetes lie side by side so that the head of one is opposite the tail of the other. Sperm then pass reciprocally into small sacs, where they are temporarily stored. This transfer is more complex in the earthworms, however, because the respective male pores are not in direct opposition; each individual forms a temporary skin canal through which the sperm flow to their respective sacs for storage. The body of oligochaetes has a swollen girdle-like structure, the [clitellum](https://www.britannica.com/science/clitellum), which serves an important function in reproduction. After the eggs have matured, a mucous tube, secreted from the clitellum, slides along the body as the worm moves backward. The stored sperm are discharged into this tube, as are the eggs when the tube slides along the section containing them. As the worm literally passes out of the tube, a mucous, lemon-shaped [cocoon](https://www.britannica.com/science/cocoon-biology) forms around the now-fertilized eggs. This cocoon serves as a kind of primitive nest, in which the young hatch.

Many [leeches](https://www.britannica.com/animal/leech) (class Hirudinea), all of which are hermaphrodites, have copulatory behaviour much like that of earthworms. Cocoons are formed in a manner similar to that described above, but in some leeches the cocoon is transparent and remains attached to the parent in which the eggs were developed. After hatching, the young leeches remain attached to the “mother” until they become independent. One African leech gives birth to live young and even possesses a special incubating chamber in its body for the developing embryos.

## Mollusks

The animals in the phylum Mollusca (e.g., clams, snails, and squid) display a diversity of reproductive behaviour. The majority of the amphineurans ([chitons](https://www.britannica.com/animal/chiton-mollusk)) and [pelecypods](https://www.britannica.com/animal/bivalve) (e.g., clams, oysters) are dioecious—i.e., individuals are either male or female. Because most species simply shed their eggs and sperm directly into the sea, individuals tend to form dense aggregations during the breeding period. The environmental factor that triggers the release of eggs and sperm has not yet been established with certainty, but, at least in a few species, after one individual has shed its sex products, the others follow in a kind of [chain reaction](https://www.britannica.com/science/chain-reaction) that is clearly chemical in nature. In some mollusks, however, such as the European oyster, the eggs are retained and brooded.

The [snails](https://www.britannica.com/animal/snail) and [slugs](https://www.britannica.com/animal/slug-mollusk) include hermaphroditic as well as dioecious species. Copulation in the hermaphroditic [land snail](https://www.britannica.com/animal/land-snail) *Helix* is preceded by a curious courtship involving a bizarre tactile stimulation. When the two partners come together, each drives a calcareous dart (the so-called love dart) into the body wall of the other with such force that it is buried deep in the other’s internal organs.

To avoid predators, some arboreal slugs [copulate](https://www.britannica.com/science/sexual-intercourse) in mid-air while each partner is suspended by a viscous thread. In the [slipper-shell](https://www.britannica.com/animal/slipper-shell) snails (*Crepidula*), which are rather sessile, all the young are males; their [subsequent sex](https://www.britannica.com/science/sex-reversal), however, is determined by their nearest neighbour. They remain males as long as they are near a female but change into females if isolated or placed near another male.

Remarkably advanced courtship behaviour in the [cephalopods](https://www.britannica.com/animal/cephalopod), particularly the [squids](https://www.britannica.com/animal/squid), involves complex visual displays of movement and changes in colour pattern. Males signify that they are ready for breeding by assuming a distinctive zebra-striped pattern, displaying their fourth arm in a flattened manner, and approaching other individuals with a jerky motion. This fourth arm in squids and the third arm in octopods, called a [hectocotylus](https://www.britannica.com/science/hectocotylus), is structurally modified for carrying [spermatophores](https://www.britannica.com/science/spermatophore), or balls of sperm. The male [cuttlefish](https://www.britannica.com/animal/cuttlefish) (*Sepia*) places the spermatophores in a pocket near the female’s mouth, from which the sperm subsequently make their way to the tubes that carry eggs (oviducts). In no squid studied thus far do either of the sexes care for the fertilized eggs, which are laid on vegetation. This is not the case with [octopuses](https://www.britannica.com/animal/octopus-mollusk), however; at least in *Octopus vulgaris*, the female [broods](https://www.britannica.com/topic/brooding) her large number of eggs (about 150,000) for as long as six weeks. During this period she aerates the egg clusters and keeps them free of [detritus](https://www.merriam-webster.com/dictionary/detritus), exhibiting remarkable behaviour for an animal that produces so many eggs. Brood care such as this is usually associated only with organisms that produce a small number of eggs.

**Arthropods**

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**Crustaceans**

With a few exceptions, [barnacles](https://www.britannica.com/animal/barnacle) are the only hermaphroditic members of the class Crustacea in the phylum Arthropoda. This is in agreement with the theory that a sessile mode of life tends to be correlated with hermaphroditism. Thus, it is not important for the organism to be near an individual of the opposite sex, but simply to be near any individual of the same species.

Some barnacles are parasitic and have undergone a radical degeneration in form. One, *[Sacculina](https://www.britannica.com/animal/Sacculina)*, is an example of the way in which the reproductive necessities of one species can profoundly affect the reproductive behaviour of another—in this case, the host. Several cells from a larval barnacle penetrate a [crab’s](https://www.britannica.com/animal/crab) body and migrate through the bloodstream until they reach the lower portion of its stomach. The cells then send rootlike projections throughout the crab’s body. When the crab molts, the barnacle protrudes a large bulbous portion of its body through the ventral (bottom) surface of the crab. If the crab is a female, its broad shell protects this structure, which contains the barnacle’s reproductive organs. The [body shape](https://www.britannica.com/science/somatotype) of the male crab, however, is much narrower and does not provide such protection. If the host is a male, therefore, the barnacle first consumes the host’s testes; at its next molt, the crab assumes the shape of a female. Should the parasite be removed, the crab regains a male appearance and regenerates its testes.

In the [copepods](https://www.britannica.com/animal/copepod) (*e.g.,* sea lice, *Cyclops*) and the [amphipods](https://www.britannica.com/animal/amphipod) (*e.g.,* beach fleas), the sexes are mostly separate, copulation is brief and without elaboration, and the female of both groups broods the fertilized eggs. The eggs of copepods are usually attached in two clusters to the rear of the female; many amphipods have a special pouch on their ventral surface for brooding the eggs. Many copepods and some amphipods are parasitic on fish and on such marine mammals as whales.

In the crustacean order [Decapoda](https://www.britannica.com/animal/decapod), which includes shrimp, crayfish, lobsters, and crabs, the sexes are separate, fertilization is mostly internal, and egg laying usually occurs shortly after copulation. In terrestrial crabs, however, the females of which migrate to [salt water](https://www.britannica.com/science/seawater) to expel the eggs, the sperm are stored, and fertilization and egg laying are delayed for several months after copulation.

[Fiddler crabs](https://www.britannica.com/animal/fiddler-crab) of the genus *Uca* and several other decapods show [territorial behaviour](https://www.britannica.com/topic/territorial-behaviour), an act that is not very common among invertebrates. As in many groups in which males defend territories, male crabs often [differ in appearance](https://www.britannica.com/science/sexual-dimorphism) from the females. Males are much more brightly coloured than the females, and one of their front claws is greatly enlarged; the mostly dull-coloured females have two small front claws. Depending on the species, males perform either simple or complex rhythmic dances in front of their sand burrows. The waving and vertical movement of the large claw is apparently species specific.

As in squids and octopuses, the sperm of primitive terrestrial arthropods—millipedes, centipedes, springtails, and silverfish—are often transferred from males to females in structures called spermatophores. During the transition from an aquatic to a terrestrial mode of life, spermatophores became necessary, particularly for those species that had not developed copulatory organs for direct transmission of sperm. Because sperm transfer in these animals is often complicated and takes considerable time, the delicate sperm would be in danger of drying up, were it not for the moisture contained in the spermatophores. It would appear, therefore, that all species that exhibit indirect sperm transfer in which spermatophores are utilized have not achieved complete independence of water.

Males of most primitive soil-dwelling arthropod species place sperm drops on threads in damp locations or use threads or chemical products to guide females to externally placed spermatophores. Most male [millipedes](https://www.britannica.com/animal/millipede) have secondary genital appendages called gonopods, by which they transfer the spermatophore directly to the genital opening of the female. One millipede actually uses a “tool” in sperm transfer; the male rounds a fecal pellet, places a drop of sperm on it, and, using its legs, passes the pellet back along its body to a point opposite the female’s genital pore. Paired body projections then are used to inject the sperm into the female, and the pellet is dropped. Males of the common bark-inhabiting millipede *Polyxenus* transfer sperm by spinning thin threads on which they place sperm drops; they then construct two parallel thicker threads on which they place a pheromone to attract the female. This chemical and tactile guidance system causes the sperm to become attached to the female’s vulva (the external part of the female’s genital organs). Males eat the sperm not picked up and replenish it with fresh sperm.

**Arachnids**

The arachnids (*e.g.,* [spiders](https://www.britannica.com/animal/spider-arachnid) and [scorpions](https://www.britannica.com/animal/scorpion)) exhibit the earliest pattern of classical courtship behaviour during which rather ritualized movements are involved. In the true scorpions this behaviour takes the form of the *promenade à deux*, in which the male holds the female by her front claws and apparently stings her in a joint near the base of the claw. The ensuing dancelike pattern apparently results from the male seeking a suitable surface upon which to deposit his spermatophore. After he deposits the spermatophore, the male drags the female over it, releasing her after the spermatophore has passed into her genital pore.

As mentioned above, many male spiders have a particular problem in approaching the aggressive and predatory female in order to deposit a spermatophore. The [hunting](https://www.britannica.com/topic/predation) behaviour of most spiders is adapted to react to the slightest movement or vibration of the [web](https://www.britannica.com/science/web), causing the spider to rush forward and bite its prey as quickly as possible. Thus, it is not surprising that male spiders have evolved fairly elaborate display movements and patterns to convey their identity. Many males are quite strikingly coloured, providing additional information about their identity. Some males approach the female only at night and vibrate her web in a highly characteristic manner, different from that caused by the struggling of a trapped animal.

**Insects**

One puzzling aspect about the courtship behaviour of insects is its sporadic nature. Most insects should exhibit behaviour involving approach, identification, and copulation. Yet, whereas male fruit flies (*[Drosophila](https://www.britannica.com/animal/Drosophila)*) often have elaborate displays preceding copulation, male [houseflies](https://www.britannica.com/animal/housefly) and blowflies (*Musca*) simply fly at any object of the proper size and attempt to copulate with it. The reason for these differences in behaviour may be that some insects do not require courtship. Males of some butterflies and moths, for example, simply wait by the pupa and copulate with the female immediately after she emerges.

It is more likely, however, that the majority of insects have fairly elaborate displays, but man is unable to sense them. The pheromones are, in fact, rather elaborate displays used as sex attractants by many insects; such sensory mechanisms are not usually perceived by man. It has been experimentally demonstrated that the reproductive behaviour of some butterfly species depends heavily on visual clues; similar experiments with other species have failed to show such behaviour. It must be realized, however, that insect [vision](https://www.britannica.com/science/vision-physiology) is quite different from that of vertebrates. Most insects have vision that is sensitive to [ultraviolet](https://www.britannica.com/science/ultraviolet-radiation) light, which man and the other vertebrates cannot normally perceive. Butterflies may appear to have identical wing [colour](https://www.britannica.com/science/coloration-biology) patterns under normal light, but, when viewed under ultraviolet light, the patterns differ drastically. Thus, insects that [mimic](https://www.britannica.com/science/mimicry) each other in order to appear identical to a vertebrate predator actually possess an unbreakable code by which each species is able to distinguish its own kind.

A reproductive behaviour that is usually misunderstood by those who have observed it is the copulation process in [dragonflies](https://www.britannica.com/animal/dragonfly). The actual copulatory organ of the male is located close to the thorax, not, as in most insects, near the tip of the abdomen. After a male alights on a plant and transfers sperm from the terminal genital opening to the copulatory organ, he seeks out a female and grasps her behind the head with claspers on his abdomen. Although the two fly in a tandem position, actual copulation occurs only when they alight, and the female bends her abdomen to receive the sperm from the male’s organ. Colour, pattern, and movement are important in species recognition. In experiments, it has been found that artificial models acceptable to male *Platycnemis* dragonflies must consist of a female head, thorax, and one wing; the model also must be moved from side to side about once every four seconds to be effective. Complete aerial mating in insects is rare, but it does occur in mayflies, houseflies, ants, wasps, and bees.

Among the [cicadas](https://www.britannica.com/animal/cicada), [crickets](https://www.britannica.com/animal/cricket-insect), and some [grasshoppers](https://www.britannica.com/animal/grasshopper-insect), females normally mate after they have been attracted to a male by [vocalizations](https://www.britannica.com/topic/vocalization) of the latter, which, in most cases, are species specific. It has been demonstrated that deafened female grasshoppers do not permit copulation. In many crickets, the specific stridulations (noises) that occur after each copulation keep the female near the male until he is ready to produce another [spermatophore](https://www.britannica.com/science/spermatophore). These stridulations also prevent the female from removing the spermatophores before insemination has been completed.

Even some butterflies incorporate [sounds](https://www.britannica.com/topic/sound-production) into their reproductive displays; in some manner, the butterfly *[Ageronia](https://www.britannica.com/animal/Ageronia)* makes a loud cracking sound when engaged in courtship. Many other insects may incorporate sound into their reproductive displays, perhaps utilizing sounds beyond the sensitivity of the human ear.

Research has revealed that [olfactory](https://www.britannica.com/science/smell) displays are widespread in insects. The sex attractants for this purpose are usually volatile pheromones. Among certain species of [butterflies](https://www.britannica.com/animal/butterfly-insect), such as the [queen butterfly](https://www.britannica.com/animal/queen-butterfly) (*Danaus gilippus*), the males possess “hair pencils” that project from the end of the abdomen and emit a scent when swept over the female’s antennae during courtship behaviour. Copulation does not occur in the absence of this chemical display.

During some stage of their development, a number of insects are either external or internal parasites on a wide variety of animals, including other insects. A particularly bizarre pattern is found in the stylopids, which belong to the order [Strepsiptera](https://www.britannica.com/animal/strepsipteran). Though seldom seen, these insects may be common internal [parasites](https://www.britannica.com/science/parasitism) of wasps and bees. The abdomen of the adult females, which never leave their hosts, consists of a bag of eggs that is concealed in the host. The forepart of the parasite, which projects from between abdominal segments of the host, is usually concealed by the host’s wings. The females of one stylopid group are apparently unique among animals in having two genital openings—both in the head—in the form of membranous windows. The larvae emerge through these openings, crawl onto a plant, and seek another host. When the host molts its old cuticle (hard skin), the larvae penetrate the soft body. Females extend their heads through the host’s abdomen and mature within the host. The males, however, leave the host, pupate in the host’s cast-off cuticle, and emerge several days later as adults. The male stylopid then seeks out a host insect and taps it on the side of the abdomen. If no female is present, the male leaves; if a female is present, she somehow signals her presence. The male then inserts his abdomen under the host’s wing and enters the genital window of the female.

It is in the orders Isoptera ([termites](https://www.britannica.com/animal/termite)) and [Hymenoptera](https://www.britannica.com/animal/hymenopteran) (bees, wasps, and ants), however, that the reproductive behaviour of insects attains its highest level of sophistication. Although dung beetles and some other insect species brood their eggs and care for the young, extreme [insect sociality](https://www.britannica.com/animal/social-insect), with its peculiar brood-care system, is found only among the isopterans and the hymenopterans. The principal [criterion](https://www.merriam-webster.com/dictionary/criterion) for such behaviour would appear to be that the female must remain with her brood until after they begin to hatch. Although the phenomenon has been intensively studied, the explanation for the evolution of extreme brood care in ants, many wasps and bees, and termites remains one of the more challenging problems in biology.

Most colonies of social insects reproduce in two ways: either sexual individuals are produced that mate and start new colonies, or the colony breaks up after reaching a certain size. Some species reproduce in both ways. In the first case, the chances of finding new sites are maximized by providing as many individuals of different sexes as possible, each equipped with appropriate guidance mechanisms. In the second, members of the parent colony explore the environment and establish a new colony where suitable.

Another example of reproduction in social insects is that practiced by many [ants](https://www.britannica.com/animal/ant). Most larvae in an ant colony develop into wingless, sterile workers. Some, however, may get more food (a point that is controversial) and grow more rapidly. These do not pupate when the other larvae do; instead, they become king-sized individuals that eventually metamorphose into sexually mature males or females with wings. Their sex, like that of the wasps and bees, depends upon whether or not the egg was fertilized by the queen.

The winged sexual forms, or [alates](https://www.britannica.com/science/alate), are produced at certain times during the year and swarm in mating flights to establish a new colony, which may actually be no more than a few hundred feet from the old colony. Actual copulation may occur either during flight or after landing on a surface. For most species of ants, it is not known whether a male will copulate with more than one female or if a female will copulate with more than one male. After copulation, the female seeks a location for a new nest and loses her wings within three to five days. Generally, two months are required to rear the first daughter workers. Some females carry a live [mealybug](https://www.britannica.com/animal/mealybug) with them on the mating flight and take it to the new colony site, where the mealybug’s offspring provide the honeydew to feed the ant’s initial offspring. Generally, however, the female ant does not provide food for her first offspring; instead, the larvae eat many of the first 100 or so eggs. This egg cannibalism decreases when there are sufficient workers to feed the larvae

# Reproductive behaviour in vertebrates

## Fishes

The reproductive behaviour of fishes is remarkably diversified: they may be [oviparous](https://www.britannica.com/science/oviparity) (lay eggs), [ovoviparous](https://www.britannica.com/science/ovoviviparity) (retain the eggs in the body until they hatch), or [viviparous](https://www.britannica.com/science/viviparity) (have a direct tissue connection with the developing embryos and give birth to live young). All cartilaginous fishes—the [elasmobranches](https://www.britannica.com/animal/elasmobranch) (e.g., sharks, rays, and skates)—employ internal fertilization and usually lay large, heavy-shelled eggs or give birth to live young. The most characteristic features of the more primitive bony fishes is the assemblage of [polyandrous](https://www.britannica.com/topic/polyandry-animal-behaviour) (many males) breeding aggregations in open water and the absence of parental care for the eggs. Many of the species in this group, such as [herrings](https://www.britannica.com/animal/herring), make what appear to be completely chaotic migrations to their breeding areas. Actually, however, each of these huge [spawning](https://www.britannica.com/science/spawning) aggregations is made up of small, coordinated parties consisting of one female and one or more males. On the other hand, a number of fishes are monogamous, form pairs, and care for the eggs or young. In courtship behaviour, in which they utilize all potential stimuli including sound, chemical, and electrical stimuli, the range and complexity of their displays are not exceeded by any other vertebrate group.

Although the sexes are usually separate, [hermaphroditism](https://www.britannica.com/science/hermaphroditism) is much more common among the bony fishes than in any other group of vertebrates. The reasons for this condition are both physiological and ecological. Whereas the developing gonads of all other vertebrates have an outer and inner layer of tissue, those of bony fishes have a simple origin that lacks any male or female elements. In terms of the evolutionary process, this type of development is likely to be more adaptable to pressures that favour hermaphroditism. When, because of one or several interacting factors, a population density reaches a low point in some species, reproduction may be limited to a low probability of contact with another sexually active individual. In such situations (e.g., very deep sea habitats, tide or stream pools) the evolution of even temporary self-fertilizing hermaphrodites would have the greatest advantage.

Similar Topics

One form of hermaphroditism fairly common in bony fishes is the protogynous type, in which the individual functions first as a female and later as a male; it is much more frequent than the reverse situation (protandrous hermaphroditism). The selective reasons for the predominance of the former are presumably associated with the relationship between smaller body size in females and the greater energy requirements needed to produce eggs. In addition, in some promiscuous mating systems, it may be selectively advantageous to be a male when the body size is large and the individual experienced, rather than small and young. Most sea basses, parrot fishes, and wrasses have this sort of hermaphroditism.

## Amphibians

Although true viviparity has been described in the African [frog](https://www.britannica.com/animal/frog) Nectophrynoides, most amphibians lay eggs. Some [salamanders](https://www.britannica.com/animal/salamander), however, retain the eggs within their body and give birth to live young. Courtship displays in frogs are almost entirely vocal, although in salamanders they may involve tactile, visual, and chemical stimuli. In the European newt *[Triturus](https://www.britannica.com/animal/Triturus)*, for example, in which mating takes place in the water, the male places himself in front of a female with his back to her. Suddenly, he executes a leap, directs a current of water at her, faces her, and bends his tail forward alongside his body; by waving his tail, he sends toward her a gentle current of water that probably carries a chemical stimulant. If the female responds by approaching the male, he turns and faces away, whereupon she touches his tail and he deposits a spermatophore, which she takes into her cloaca, a common passageway into which waste products and reproductive cells are discharged.

Most frogs and salamanders do not show brood care, but there are exceptions. In the European [midwife toad](https://www.britannica.com/animal/midwife-toad) the male rather than the female carries the sticky eggs on its hindlimbs. In a number of Neotropical frogs, the male carries the eggs under a flap of skin on its back. In some species, the young (tadpoles) cling to the back of the male by using their sucker-like mouths.

## Reptiles

Reptiles are the first vertebrates that, in an evolutionary sense, have evolved an egg that is truly independent of water. Indeed, many snakes and lizards have even gone beyond this stage and have attained complete viviparity. It is difficult to generalize about reproductive behaviour in the reptiles because the various groups differ from each other in the sensitivity of their receptor organs. In many [turtles](https://www.britannica.com/animal/turtle-reptile), for example, the males are territorial and are very aggressive during the breeding period. Courtship behaviour involves mainly tactile stimuli, but olfactory clues are also important. It has been recorded that the [wood turtle](https://www.britannica.com/animal/wood-turtle) (Clemmys) actually emits a low whistle during courtship. Turtles usually bury their eggs and do not brood them.

[Lizards](https://www.britannica.com/animal/lizard) appear to use almost every sensory mechanism in their reproductive activities. The nocturnal [geckos](https://www.britannica.com/animal/gecko) employ vocalizations, in addition to tactile and olfactory stimuli. [Skinks](https://www.britannica.com/animal/skink) such as Eumeces rely heavily on olfactory clues. Lizards of the large family [Iguanidae](https://www.britannica.com/animal/iguanid), on the other hand, are almost entirely diurnal creatures and utilize, in the main, visual displays, some of which are the equal in complexity to any known among the vertebrates. Many, such as the [anoles](https://www.britannica.com/animal/anole), are equipped with a throat flap (dewlap) that is often brightly coloured and specifically marked; it is utilized both in courtship and territorial defense. The skinks and a number of other lizards are known to guard their eggs.

In general, the reproductive behaviour of [snakes](https://www.britannica.com/animal/snake) is not well known. The tongue is apparently an important sense organ for receiving olfactory and other chemical stimuli. The males of some snakes have characteristic skin papillae (nipple-like projections) on the throat; the fact that they rub the papillae over the female’s body suggests that tactile stimuli are also important to reproduction. In [boas](https://www.britannica.com/animal/boa-snake-family), the [rudimentary](https://www.merriam-webster.com/dictionary/rudimentary) pelvic bones serve as “claws” for lifting the hind end of the female and for producing a vibration that is said to be important in the process of copulation. Some snakes, the pythons in particular, incubate and guard their eggs.

The bellowing roars of male [alligators](https://www.britannica.com/animal/alligator) serve to establish breeding territories and apparently also to attract the females. Female crocodiles remain in the vicinity of their nest and will defend it vigorously.

## Birds

Although all birds [lay](https://www.britannica.com/topic/brooding) eggs, it is curious that they do so, because the time of highest mortality in most birds usually occurs during the egg-laying period. Apparently, birds lack some adaptation that would permit them to become viviparous.

Most birds build a nest and [incubate](https://www.britannica.com/science/incubation-of-eggs) their eggs, but the incubator birds and such brood parasites as cuckoos are among the exceptions to this rule. Many females that lay a fixed number of eggs are referred to as determinant layers. The [pigeons](https://www.britannica.com/animal/pigeon) and [doves](https://www.britannica.com/animal/dove-bird) are outstanding examples of this behaviour; for some as yet unknown reason, they never lay more than one or two eggs. Other species are often referred to as indeterminate layers because, in the absence of a suitable stimulus, they continue to produce eggs. More often than not, this stimulus is the presence in the nest of a certain number of eggs. Such behaviour is clearly adaptive—if eggs are lost for some reason and if other environmental stimuli are present, the missing eggs are replaced. The distinction between determinate and indeterminate layers is often blurred, for many indeterminate layers will not replace more than one or two missing eggs.

The duration of egg incubation varies from as little as nine days in some tropical perching birds to as long as 80 days in some albatrosses. In most species that form pairs, both individuals incubate and feed the young, but the female usually has the greater share of the burden. Among the exceptions to this behaviour pattern are the tinamou (partridge-like game birds), ostriches, some gallinaceous species (e.g., pheasant, grouse, turkeys), and [phalaropes](https://www.britannica.com/animal/phalarope). In the phalaropes, the role of the sexes is largely reversed: the females are more brightly coloured than the males and, not surprisingly, are the aggressive ones in courtship and in territorial defense; incubation is carried out solely by the male, but the female aids in feeding the young.

Because many birds begin incubation with the laying of the first egg in the clutch, the eggs hatch at different times. This strategy is often employed by species whose food supply for the young may vary in abundance over a fairly short period. Hence, should food suddenly become scarce, only the smallest chick or chicks will starve rather than the entire clutch. Species in which the young hatch in a relatively well developed, almost independent state tend to have very large clutches, as in many gallinaceous birds. In this case, it might be said that the ultimate size of the clutch is regulated by the abundance and quality of the food available to the female as she produces eggs. The same explanation also accounts for clutch size in parasitic birds—i.e., those that lay eggs in the nests of other species. The breeding densities of birds vary from one pair in many square miles, as in some birds of prey, to such species as the fulmar, which forms colonies numbering as many as 250,000. Some colonies of the African weaverbird (*[Quelea](https://www.britannica.com/animal/quelea)*) have been estimated to exceed 1,000,000 individuals.

One interesting aspect of reproductive behaviour in birds, possibly peculiar to them and to some mammals, is that many courtship displays are learned, or at least perfected through practice, from the parents. An example is the [learning](https://www.britannica.com/topic/learning) of [birdsongs](https://www.britannica.com/topic/birdsong-animal-communication). It has been shown in some cases that when chicks are switched from the nest of one species to that of another, they learn some and perhaps all of the songs of the foster parents and do not develop their own species’ [vocalizations](https://www.britannica.com/topic/vocalization). When mature, such birds often prefer to choose as mates individuals of the same species as their foster parents’ rather than those of their own species.

Courtship stimuli in birds are mostly visual and auditory, but it is possible that odour may be important in some petrels and shearwaters. As previously mentioned, most birds form [pairs](https://www.britannica.com/topic/pair-bonding). In these and in many that do not, the males engage in communal, or lek-type, [displays](https://www.britannica.com/topic/display-behaviour) on a common courtship ground, such as the familiar strutting grounds of turkeys and many grouse. In addition, there are the incredibly bizarre communal dances of the birds of paradise; the jungle-floor dancing of the cock of the rock; the pasture display grounds of the shorebird, the ruff; and the forest arenas cleared for displaying purposes by the tiny manakins. Many of these display areas are used for many years; in some manakins, for example, certain cleared arenas have existed continuously for at least 30 years. In most lek species, the males are usually brightly coloured, and the females are rather dull in appearance. An exception occurs in some hummingbirds, the so-called hermits, in which both sexes are rather dull in coloration and in which the males group together in singing assemblies.

## Mammals

Most mammals give birth to live young. The outstanding exceptions are the egg-laying [monotremes](https://www.britannica.com/animal/monotreme) of Australia, the [platypus](https://www.britannica.com/animal/platypus) (Ornithorhynchus) and the [echidnas](https://www.britannica.com/animal/echidna-monotreme) (spiny anteaters). In the duckbill platypus, a brief courtship involving a chase in the water precedes copulation. The two eggs that are produced are placed in a burrow and hatch in eight to 10 days. In the reproductive behaviour of the spiny anteater (Tachyglossus), the female apparently lays her single egg directly into her pouch.

As already mentioned, another general aspect of reproductive behaviour in mammals is the [estrous](https://www.britannica.com/science/estrus) cycle, knowledge of which is essential to an understanding of the mechanisms involved in the reproduction of any mammalian species. In most cases, females are responsive to males only during that portion of the estrous cycle when they are in heat; that is to say, when one or more [eggs](https://www.britannica.com/science/egg-biology) have [broken out of the ovary](https://www.britannica.com/science/ovulation) and are in the process of descending to the uterus. The factors causing this event vary significantly, but in some such as rabbits and cats, copulation itself is the main stimulus. In general, however, those mammals, particularly the large ones, that live in temperate areas—bears, dogs, wolves, foxes, seals, and some deer and antelopes, for example—have one estrous cycle per year. Mammals that live in warmer zones, such as some areas of the tropics, tend to have more than one estrous cycle per year. The sexual cycle in males, the height of which in some forms is referred to as the rut, is, not surprisingly, usually correlated with that of the females. The males of many species of domestic mammals, however, seem to be capable of copulating at almost any time of the year.

Another general aspect of mammalian reproductive behaviour is that they do not normally form pairs. Exceptions occur in certain carnivores and in some primates, in which parental care is divided between the sexes. As in many insects, the courtship behaviour of most mammals does not appear to be elaborate; but, just as in the former group, most mammals (humans are an exception) have an [acute](https://www.merriam-webster.com/dictionary/acute) sense of smell. It is possible, therefore, that many of the chemical attractants wafted into the air by receptive females are actually courtship displays that are more complex than has been realized. This is not to say, of course, that visual, auditory, and tactile displays do not occur. Many [deer](https://www.britannica.com/animal/deer) and [antelopes](https://www.britannica.com/animal/antelope-mammal), for example, have rather complex ritualized visual displays employing such movements as strutting and arching of the heads, as well as conspicuous colour patterns. Males in many species discharge urine on females as a preliminary to copulation. Tactile and auditory displays have been shown to be important in aquatic mammals, such as porpoises and whales.

In addition to a number of mammalian pheromones, other odour effects occur in mammals that, aside from their simple advertising value, have an important influence on reproductive behaviour. It has been shown that, when a recently impregnated female [mouse](https://www.britannica.com/animal/mouse-rodent) is exposed to the odour of a male other than the one with which she has mated, implantation of the egg in the uterus often fails; as a result, there is a rapid return to estrus. The odour of a strange male may signify to a female rodent an unfavourable situation in which to raise young, inasmuch as a number of male rodents attempt to attack offspring not their own. Although it is not yet certain, there might be an adaptive explanation for this behaviour. The population fluctuations of rodents have attracted much attention, and, perhaps correctly, studies have focussed on the ecological [parameters](https://www.merriam-webster.com/dictionary/parameters) of these fluctuations; for example, it has been demonstrated in the laboratory that certain behavioral mechanisms involving odours exercise profound control over the reproduction and population levels of rodents. It has also been shown that the odour of mice can stimulate the production of hormones that cause a decrease in the reproductive capacity of other mice. In another study, estrus was suppressed and many pseudopregnancies developed when four or more female mice were grouped together in the absence of a male. These results offer a partial explanation for the reduction of [population](https://www.britannica.com/science/population-biology-and-anthropology) growth in rodent colonies with high population densities.

## Evolution of reproductive behaviour

There is a popular tendency to think of primitive animals (in a phylogenetic or descent sense) as lacking “elaboration”; i.e., that the animals of earlier geological periods had simpler displays or perhaps lacked crests or pheromones or elaborate communal displays in comparison with their present-day counterparts. There is no a priori reason for this belief. The [fossil record](https://www.britannica.com/science/fossil-record) indicates that the societies of which these animals were a part were as [diverse](https://www.merriam-webster.com/dictionary/diverse) and complex as those in which their relatives now live; certainly their display [repertoires](https://www.merriam-webster.com/dictionary/repertoires) should have been equally complete. This is not to say, however, that the primitive forms of reproductive behaviour used the same displays for courtship as do the modern forms.

## Displays

It has been pointed out that, in general, animals have relatively few displays; in addition, it has been deduced that the relative stability of displays is a [dynamic](https://www.merriam-webster.com/dictionary/dynamic) equilibrium—that is, new ones are gained and old ones are lost at about the same frequency. Displays are lost when they no longer convey a selective advantage to the individuals using them; that is, when they are no longer effective in promoting the behaviour that seeks to maximize gene survival in the next generation.

New displays, on the other hand, generally arise by ritualization of previously existing behaviours or functions; that is, when a selective advantage [accrues](https://www.merriam-webster.com/dictionary/accrues) to those individuals who, to convey information, use certain behaviours or functions in a manner that is either partly or totally different from their original purpose. [Pheromones](https://www.britannica.com/science/pheromone), for example, are usually derived from compounds that are natural breakdown products of body metabolism, such as the compounds in urine. Thus, urine, as the [precursor](https://www.merriam-webster.com/dictionary/precursor) of these chemical sex attractants in insects, functions for display purposes, which is far removed from its basic excretory function.

[Darwin](https://www.britannica.com/biography/Charles-Darwin) proposed a theory of [sexual selection](https://www.britannica.com/science/sexual-selection) to account for the presence in animals of displays and functions that apparently were not related to survival. He pointed out that two general concepts were involved. First, the evolution of such characteristics as the larger size of males in many species and the development of horns and antlers in mammals could be accounted for by their usefulness in fights between males for their sexual possession of females. This concept has been termed intrasexual selection. For such colourful male structures as the plumes of birds of paradise and the tails of peacocks, Darwin suggested that they resulted from the [cumulative](https://www.merriam-webster.com/dictionary/cumulative) effects of sexual preference exerted by the females of the species at the time of mating. This second concept has been termed epigamic selection.

A displaying male has been known to convey information about his [relative fitness](https://www.britannica.com/science/Darwinian-fitness); that is, his ability, with respect to other displaying males, to maximize the survival of his genes into the next generation. Both the brightness of his coloration and the frequency with which he struts say something about the effectiveness of his genes to produce a “healthy” individual. Once this correlation takes place, selection favours those females who are able to choose the “most fit” males. Correspondingly, sexual selection intensifies the signals up to the point at which any further elaboration of those signals would result in a loss of fitness. When selection goes beyond this point, the male, because of his elaborate ornamentation and other displays, is more likely to suffer from predation before he has the opportunity to reproduce.

## Sexual selection

The discussion concerning courtship displays leads naturally to the concept of sexual selection. Why do the males of some species possess elaborate displays? Why, in fact, do some species “elect” to utilize one mating system, say a monogamous one, while others “choose” a polygamous one? It has been suggested that many courtship displays and mating systems, particularly those involving polygamous systems with communal displays in a common courtship area, have an epideictic function—that is, they provide information as to the number of like individuals in a locality. The animals then act according to the information received, often by reducing their reproductive output. Because this concept implies that natural selection is acting for the good of the species rather than for the good of the individual, it has been called [group selection](https://www.britannica.com/science/group-selection). This concept has provoked considerable controversy for two reasons: first, there is no known mechanism by which group selection can function; second, as mentioned earlier, the pertinent behaviours involved can be more simply explained in terms of Darwinian selection dealing with individuals rather than groups.

In a number of [polygynous](https://www.britannica.com/topic/polygyny-animal-behaviour) (mating of one male with more than one female) and promiscuous species, adult females outnumber adult males, sometimes by a factor of five or more. It has been erroneously suggested that this sexual imbalance is the cause of the polygynous mating system, in which one male has several female partners. It has been demonstrated, however, in all polygynous species so far studied, that the ratio of males to females is 50:50 at the time of birth; in many cases, this ratio persists until the cessation of parental care. Therefore, it is the polygynous relationship that causes the imbalance, not vice versa: because sexual selection is the dominant factor in a polygamous and promiscuous species, it results in a greater mortality of males than of females.

Because one male can impregnate many females, thus lowering the selective value of an individual male, females are more valuable than males in an [evolutionary](https://www.britannica.com/science/evolution-scientific-theory) sense. It can be seen, therefore, that sexual selection always favours a polygynous and promiscuous system unless it is disadvantageous to the females, as it is in most birds. In most mammals, however, polygyny is the dominant mating system because the male is not needed for parental care. Therefore, [monogamy](https://www.britannica.com/topic/monogamy) is favoured over [polygamy](https://www.britannica.com/topic/polygamy-animal-behaviour) only when some environmental resource (food, for example) is limited and when the maximum survival of young requires the care of both parents. As in all other aspects of reproductive behaviour, the type of mating system that is employed by a species is the result of [natural selection](https://www.britannica.com/science/natural-selection)