

## Courtship Rituals



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## Courtship and Mate Choice

Courtship consists of a wide variety of behaviors performed with the intention of achieving an opportunity to mate. Successful courtship results in a pair of animals copulating. Both members of the pair participate in copulation, and this often leads to situations where one individual must persuade the other to choose them as their mate. This process of persuasion occurs through courtship rituals. In some cases, courtship behaviors can be so consistent among members of a species that they are referred to as courtship rituals. These behavioral displays vary across species, but they share the central role of providing a means through which a suitor can advertise their qualities to potential mates. Through performance and evaluation of these displays, individuals engaged in courtship choose their mates; and successful courtship can lead to copulation and the formation of social pair bonds. Pair bonding behaviors and the associated social connection can thus reinforce a mate choice that began with

the performance of courtship behaviors. Individuals often incorporate a combination of bond-forming behaviors and courtship rituals to choose a mate, as social bonds may influence the effectiveness of the courtship ritual.

Courtship rituals can be performed by either males or females. Across species, most rituals involve males performing ornate behaviors to attract the attention of females and court them as potential mates (Darwin 1871). In those cases, the female serves as the evaluator of the quality of a male's displays (Zahavi 1975). Although this can make it appear that females have the sole choice in mate selection, this is not the case, as the initiation of courtship reflects a preference expressed by the male; and mating requires agreement of both participants. Suitors select a recipient of their courtship displays, and receivers evaluate those advertisements and decide whether to accept the suitor's courtship. Therefore, elaborate displays and ritualized behaviors can be important aspects of successful courtship, but they are often only one component in what is ultimately a mutual mate choice.

## Evolution and Importance of Courtship

Sexual reproduction and the variation that it can introduce are key elements in the process of evolution. Sexually reproducing organisms pass their genetic content to the next generation, propagating their species and enabling it to persist through

future generations. Sexual reproduction is very common across species. As the saying goes, birds do it, bees do it, and the majority of all eukaryotic organisms engage in sexual reproduction (Goodenough and Heitman 2014). Sexual reproduction is evident in both plants and animals, but courtship rituals are behaviors that are performed across animal species. Therefore, this text will focus on animals in our consideration of courtship behaviors and how they influence reproductive success.

In order for sexual reproduction to occur, each participant must locate and mate with another member of their species. Factors like opportunity, competition, and attraction can all influence courtship and mating success. It is advantageous for an individual to mate with a partner with high evolutionary fitness, meaning that they are well adapted to survive and produce viable offspring in their environment (Zahavi 1975). It is often said that animals express a “preference” when they choose their mate, but this term can be difficult to define. For example, in most species, individuals do not randomly mate. This has given rise to the idea that certain traits are preferred more than others. Suitors with the preferred trait will leave more offspring, and the numbers of individuals expressing that trait will increase in frequency throughout the population. As Darwin noted in his studies of sexual selection, “when we see many males pursuing the same female, we can hardly believe that the pairing is left to blind chance – that the female exerts no choice, and is not influenced by the gorgeous colors or other ornaments with which the male alone is decorated” (Darwin 1871). This reveals how tempting it can be to think that animals possess a humanlike sense of aesthetics, and the advertisement and appreciation of “beautiful” or “high quality” traits drive courtship and reproduction. The cognitive experiences of animals are the focus of ongoing research, but it remains largely unknown what mental or physiological states occur when an animal encounters a member of its species that expresses some preferred trait. Nonetheless, those traits can be strongly predictive of reproductive success; and that is what is referred to as the

traits of the suitors preferred by the receivers of those courtship behaviors.

When one or both members of a pair actively choose a mate from many options, sexual selection occurs. Sexual selection arises from differences in reproductive success that are caused by differences in access to mates (Darwin 1871). Differences in access can occur because of many different factors such as males competing with one another to gain access to mates, or females only granting reproductive opportunities to males that express an abundance of certain preferred traits. Anatomical features such as size, coloration, and other forms of ornamentation can affect this choice, but behavioral displays can also play a very significant role in affecting which individuals are chosen as mates. The strong link between mate preference and the expression of certain behavioral displays is thought to be a driving force in the emergence of courtship rituals.

Courtship rituals vary greatly depending on the preferred traits which they advertise. Traits can be advertised through many different behaviors including singing, dancing, and demonstrating physical vigor through fighting or other challenging behaviors. Complex rituals can allow for many attributes to be displayed and evaluated at once. Observers can gain insight into the sender’s genetic composition, cognitive ability, health, social status, and/or access to specific resources through the quality of a display performed by a potential mate. This gives the observer a great amount of information in a compact and succinct manner. Through displays, the sender attempts to communicate both the quality of their attributes and their availability in order to influence the behavior of the observer. The observer, in turn, analyzes those displays, evaluates their quality, and uses that information as the basis of their decision about whether the sender will be selected as a mate and granted reproductive opportunity.

## Male and Female Roles in Courtship

Courtship rituals occur between two members of the same species and influence the likelihood of mating success (Darwin 1871; Zahavi 1975).

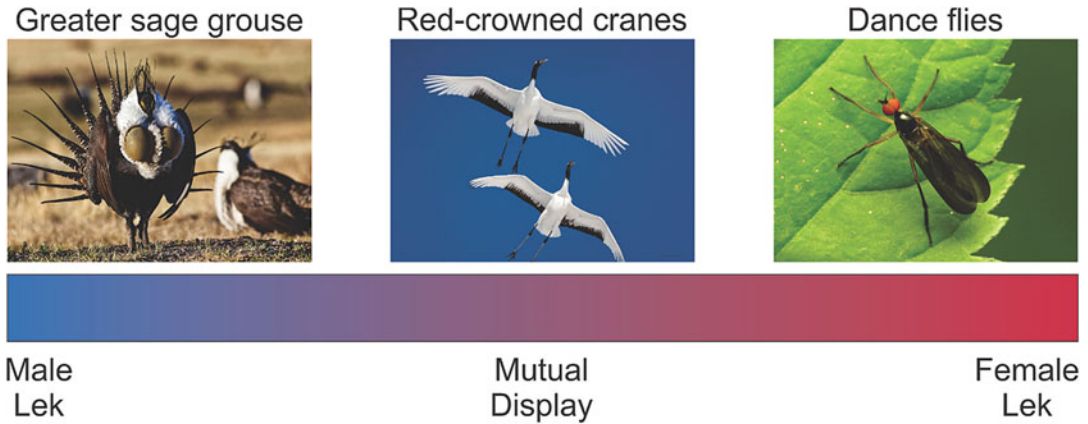
Those participants are typically a male and a female, with the male acting as the primary sender of courtship behaviors and the female as the primary receiver, but both parties often make a choice in order for a courtship ritual to be successful (Johnstone et al. 1996). If a potential sender does not judge the potential receiver to be of sufficient quality to be considered as a potential mate, he will not display. If the receiver does not judge the sender and his signal to be of sufficient quality, she will not show preference or grant reproductive access. If both sender and receiver evaluate the other as high quality, then courtship succeeds, and mating may follow. In that way, mate choice is typically a mutual decision. In the preceding example, the male was portrayed as the sender and the female as the receiver, but there was also a portion of that scenario when the female also performed behaviors to solicit copulation or otherwise indicate her preference for the male. Therefore, both participants acted as sender and receiver at different times in the process, but the male played the role of the sender more than the female.

In the preceding example, both participants made a choice, and those choices were evident in the behaviors expressed by each participant. Therefore, it would be incorrect to say that either participant was the sole sender or receiver or that either was the only one that made a choice. In light of these nuanced contributions by both participants, it can be useful to think of the roles of signaler and receiver as lying along a spectrum between the two sexes (Fig. 1). A specific example of courtship behavior can be characterized by its position along that spectrum as determined by the amount of display or choice made by the male or the female in that example (Fig. 1). Lek mating, where many of a single sex compete or display for members of the opposite sex who are observing them, can be used to illustrate the extremes of the spectrum (*lek* is adapted from the Swedish work *lekställe*, meaning “mating ground”) (Fig. 1).

Male sage grouse provide a classic example of male lekking (left end of the spectrum in Fig. 1). Male sage grouse meet in ancestral areas to lek and strut for females (Wiley 1978). They erect their tail feathers and inflate large, yellow

esophageal sacs, which swell and make popping sounds when the air is released, to attract attention (Wiley 1978). They repeat this every morning for weeks, guarding their position in the lek from other males, as central locations offer better mating opportunity (Wiley 1978). At the conclusion of this competition, a small percentage of male sage grouse are selected by the vast majority of females as mates (Wiley 1978). Thus, sage grouse are a classic example of a male lekking system. Lek mating can also occur in the context where females compete to be selected by male observers (right end of the spectrum in Fig. 1). For example, many species of dancing flies rely on female displaying leks. In these species, females gather in swarms and display, allowing males to observe their behavior and choose their mates from among the group (Funk and Tallamy 2000).

Lek mating systems illustrate the extremes of either male or female choice, but many species do not conform to these extreme examples. Mutual displays, where both sexes participate to a large degree in the courtship ritual, reflect the middle ground (middle of the spectrum in Fig. 1). In these cases, both the male and female serve as signaler and receiver, advertising their own qualities while also evaluating the qualities of their potential mates. Success of the courtship ritual depends on both participants choosing each other. For example, in the pre-copulation displays of red-crowned cranes (middle of the spectrum in Fig. 1), both the male and the female perform an elaborate combination of calls, bill movements, and wing flapping before they copulate (Masatomi and Kitagawa 1975). In this way, both the male and female display to one another, with neither serving as the primary sender or receiver, and both evaluate the quality of their potential mate (Masatomi and Kitagawa 1975). Just as there are differences at the extremes of the spectrum, there can also be variation within the intermediate portion of that spectrum. In most species, males act as the primary senders, and females act as the primary receivers. There can be exceptions to this trend, such as gray phalaropes and dance flies, in which females act as the primary senders and males act as receivers (Funk and Tallamy 2000; Ridley 1980). These exceptions highlight the fact that courtship



**Courtship Rituals, Fig. 1** The spectrum of displays among males and females. Male display and female choice are illustrated by male leks in greater sage grouse (left; Wiley 1978; image: Greater\_sage-grouse\_(Centrocercus\_urophasianus).jpg by the Bureau of Land Management), mutual display and choice are illustrated by red-crowned cranes (middle; Masatomi and Kitagawa 1975; image:

Red-crowned-overhead DSC9943.jpg by Casumma/CC BY-SA), and female display and male choice are illustrated by female leks in dance flies (right; Funk and Tallamy 2000; image: Dance Fly – Flickr – treegrow.jpg by Katja Schulz from Washington, DC, USA/CC BY). All images were obtained through Wikimedia Commons, licensed for reuse through <https://creativecommons.org/licenses>

rituals are unique to each species. Differences among species can make it challenging to generalize about the nature of courtship rituals, and they make it clear that any study of courtship rituals must include consideration of the context in which they occur.

### Physiological Components of Courtship

Many species have developed physical adaptations that serve in signaling information. These adaptations, called ornaments, come in all sorts of shapes and colors (Darwin 1871; Zahavi 1975). The vibrant plumage of many birds, the colorful abdomen of jumping spiders, the pinnate leg scales of female dance flies, and the crimson combs of male jungle fowl are just a few examples of ornamentations (Dunn and Cockburn 1999; Frith and Frith 1987; Lenz 1994; Funk and Tallamy 2000; Ligon et al. 1990; Lim and Li 2004; McDonald 1989). In many cases, ornaments reflect both the genetic and nutritional quality of the signaler. High-quality ornamentation requires the associated genes to produce consistent, complex results. Similarly, extreme ornamentation reflects a healthy lifestyle that allows

the signaler to expend excess energy and resources to support the development of their ornaments (Zahavi 1975). Thus, genetics define the axis along which the ornament can be developed, but it is experience that determines the degree to which that signal is actually expressed. Fairy-wrens provide a great example of this. The plumage coloration of superb fairy-wrens acts as an honest signal for both the age and nutritional quality of the males displaying those feathers (Dunn and Cockburn 1999). Male superb fairy-wrens molt and grow their new feathers months before the breeding season (Dunn and Cockburn 1999). Older males and nutritionally healthy males molt and begin expressing those colorful feathers much earlier than young or unhealthy males (Dunn and Cockburn 1999). This advantage in timing allows them to begin displaying to females earlier in the breeding season and thus display to females for a longer duration throughout the season, giving them an advantage in terms of claiming territory and attracting mates (Dunn and Cockburn 1999). Thus, the nature of the courtship that females receive is a reflection of the age and nutritional status of the males performing those courtship behaviors.

There are many examples of courtship displays that rely on the receiver's vision to detect information; however, the traits and reproductive status of a potential mate can also be advertised through signals that are detected in other ways. For example, there are nonvisual signals that have profound impact on reproductive behaviors, such as the production of pheromones. Because pheromones are invisible, the importance of these signals for other species can be easily overlooked. Pheromones are small molecules that are produced and released by one individual and are detected by another member of the same species. Like visible ornaments, the quality of their signals can depend on both genetics and nutritional status. For example, female thynnine wasps are wingless, and they perch on the tips of plants while releasing strong pheromones that attract males (Alcock and Gwynne 1987). Winged males can detect those pheromones in very small concentrations, and they use that information to follow the gradient of increasingly greater concentration until they arrive at their source. Pheromones serve as a signal that guides males to females, and the arrival of the male is often followed by copulation (Alcock and Gwynne 1987). Thus, reproductive signaling can occur through a variety of different behaviors and sensory modalities.

## Behavioral Components of Courtship

Anatomical or physiological ornaments can require many generations to emerge and develop as indicators of an individual's status. Behavior, on the other hand, is much more plastic, allowing behavioral aspects of advertisement and courtship to emerge much more rapidly than structural aspects. Not only are behavioral aspects of courtship very flexible, they are also able to indicate additional aspects of the displayer's status. For example, aspects of cognitive ability and social standing can be displayed through behaviors in ways that may be very difficult or impossible to communicate through physical parameters of ornamentation. This is why behavior is such an important indicator of mate quality, as it reveals characteristics that are acquired within the

displayer's lifetime and is thus directly related to that individual rather than an assemblage of individuals across generations. For example, zebra finches sing to attract females. Young males learn their songs from adult male tutors during early development, and the nutrition that the young bird receives during that developmental phase impacts the quality of his song performance then and throughout his life (Brumm et al. 2009). Thus, the quality of a male's song indicates not only his ability to perform that song in the present but also his life history in terms of juvenile nutrition and social environment, as well as his skill in learning, memorizing, recalling, and rehearsing that song.

Courtship rituals often combine ornamentation and behavior to increase the amount of information signaled to potential mates. For example, intrasexual fighting is common in courtship rituals. These agonistic behaviors use direct competition to indicate the strength and health of the fighters. While the structures used to fight are often anatomically determined, animals must be healthy, reflecting good nutrition; skillful, reflecting good cognition; and strong, reflecting good genetics, in order to win the fight. While these behaviors often do not directly lead to mating, they are correlated with mating success, as victors are more likely to gain an opportunity to mate. Thus, fighting behavior can communicate information about multiple attributes, including physiological traits that an observer would not be able to detect directly. In jungle fowl, male fighting success is correlated with the amount of testosterone the male produces (Ligon et al. 1990). Other testosterone-dependent traits, like comb color and size, are evaluated by females of other species and are also important for mating success (Ligon et al. 1990). This correlation between a physiological trait and mating success is thought to emerge because males with more testosterone are able to fight competitors and court females with higher rates of success (Ligon et al. 1990).

Another form of physical courtship ritual common across the animal kingdom is dancing, in which rhythmic movements of the body are used as a signal. Dancing allows the signaler to display

their physical prowess to the evaluator. Ornaments are often displayed during these courtship rituals, signaling additional attributes. Jumping spiders, for example, dance to attract females. When attempting to court, the male raises his body and flexes his vibrant abdomen while arching his legs and vibrating his palps (Lim and Li 2004). He then will skitter toward the female and tap her legs to solicit copulation (Lim and Li 2004). Male superb birds-of-paradise are famous for their elaborate, multi-step displays. The first step involves a male sleeking his plumage while crouching to attract females to his area, bowing and displaying his unerect cape to any nearby individuals (Frith and Frith 1987). After a female lands on his perch, the male spreads his tufts and cape, creating a black oval and thrusting his brightly colored breast shield forward (Frith and Frith 1987). Iridescent pseudo-eyes above his real eyes and clicking sounds made by wing movements accompany the male as he dances near the female by hopping around her, calling, or displaying his bright yellow mouth coloration (Frith and Frith 1987). If the female finds the dance attractive, the two will copulate (Frith and Frith 1987). This dance requires strong males with healthy genetic backgrounds and nutritional experience to produce these vigorous dances and vivid ornaments.

Many animals use auditory stimuli to signal information, but none are as famous for the Passerine songbirds. Songbirds sing to communicate. Their songs, unlike anatomical ornaments, must be learned and practiced. Males learn their songs during juvenile development by copying song elements performed by adult tutors, and they rely on hearing throughout their life to practice and maintain the quality of those songs. In this way, a male's song, like that of the male zebra finch, provides insight into not only the present health of the bird but also that male's ability to learn and perhaps other aspects of his cognitive ability (Boogert et al. 2011; DuBois et al. 2018; Sewall et al. 2013). Developmental stress, poor health, and many other factors can negatively impact the male's song quality, making it an

important signal for use in female evaluation of the singer as a potential mate (Brumm et al. 2009).

Courtship rituals can also incorporate features of the environment to reveal the signaler's resourcefulness and skill. For example, displayers can advertise their ability to claim and defend territory, as well as their ability to provide resources. A common form of these rituals involves nest building. Male pufferfish construct complex sand circles, ridged with sand ripples, decorated with shells, and built using small, soft sand particles (Kawase et al. 2013). These nests take days for the male to form and refine, showing the quality of the male's territory and his skill in building a shelter to provide for potential offspring (Kawase et al. 2013). Bowerbirds, however, are possibly the most famous nest builders. Regent bowerbirds build elaborate bowers, consisting of raised walls made of sticks that come together to form a tunnel-like structure, and the males decorate those structures with objects they find (Lenz 1994). These are often very colorful objects, such as snail shells, bright leaves, and pieces of blue plastic; and the decorations are presented to females as part of the courtship ritual (Lenz 1994). Female bowerbirds visit males with quality bowers for longer periods of time, reflecting the female's preference (Lenz 1994). Other species also incorporate found objects into their courtship rituals, such as gifts of food presented by male dancing flies to females immediately prior to copulation (Funk and Tallamy 2000). These gifts are so nutritional that females in some species of dancing flies have lost the ability to hunt and are thought to depend on these nuptial gifts (Funk and Tallamy 2000).

In addition to forms of courtship in which a specific behavior serves as the primary means of display, many forms of courtship ritual consist of a combination of displays. For example, brown-headed cowbird males sing while puffing their chests and flapping their wings to attract females (Cooper and Goller 2004). This "song and dance" exertion often causes pauses in their song (Cooper and Goller 2004). Males of higher physical capability can continue with fewer pauses, and this is



thought to indicate that they have the motor and respiratory capacity to handle the exertion. (Cooper and Goller 2004). Long-tailed manakins also offer a great example of complex multimodal mating rituals. These vibrant, lekking birds work in teams to attract females (McDonald 1989). One high-ranking (alpha) male and another subordinate (beta) male first attract females with a chorus of calls (McDonald 1989). Once the female has been drawn into the area and can observe their behavior, they engage in a series of backward jumps over each other while singing and fluttering in the air (McDonald 1989). If the female is receptive, the alpha may solo display then copulate (McDonald 1989). This combination of synchronized singing and dancing is especially unusual among mating rituals, as multiple males work together to display; but only one gets an opportunity to mate (McDonald 1989). The alpha male signals his health and genetics through his bright plumage, consistent calls, and dance, while he also displays his social status in his duet and synchronized dancing (McDonald 1989). The beta, in turn learns and practices the proper method of singing and dancing and can eventually become an alpha when he is older and more skilled (McDonald 1989).

Behaviors that comprise courtship rituals can also have an impact beyond direct courtship. For example, courtship rituals can help form and maintain social bonds between two individuals. Gray phalaropes use many aspects of their courtship behaviors to bond with a male days before copulation occurs (Ridley 1980). Black swans perform the triumph dance whenever one of the pair chases out an intruder, and this behavior increases their pair bond even though it is not always followed by copulation (Kraaijeveld et al. 2004). Alpha and beta male long-tailed manakins likewise form a complex social bond through displaying together (McDonald 1989). Finally, these displays can also advertise the signaler's quality to potential competitors. In highly competitive courtship rituals, like leks, high-quality displayers dissuade competitors and take optimal positions through the use of their displays (Wiley 1978; Jukema and Piersma 2006).

## Dishonesty in Courtship Rituals

The preceding examples illustrate that courtship signals can have a number of benefits for the sender. In many cases, they are also informative and thus beneficial for the receiver. However, not all advertisements are honest signals of the sender's traits. Most courtship behaviors are reliable indicators of the quality of the associated sender. These are called "honest" signals, and they enable the receiver to form an accurate assessment of the sender's quality. Displayers of certain species, however, have developed methods of using dishonest signaling to mate with evaluators. For example, male cuttlefish can change their color and shape. Males typically display bright patterns to females in order to court them and then guard their mates from rival males (Norman et al. 1999). Small males, however, cannot compete with larger males. Small males sometimes use deceptive signaling to copulate with females. In these cases, a small male mimics the mottled appearance of a female. He uses this deception to enter the territory of a male that would otherwise chase him off (Norman et al. 1999). The deceptive male can then attempt copulation with the guarded female when the large male is distracted (Norman et al. 1999). Male mourning cuttlefish take deception one step further. A male of this species can display male courtship markings to a female on one side of his body while simultaneously displaying female markings to a rival, territorial male on his other side (Brown et al. 2012). In this way, deceptive males can court protected females while avoiding retribution (Brown et al. 2012).

One of the most impressive examples of deceptive rituals lies with the shorebirds called ruffs. Ruffs typically protect small territories, and males engage in lekking to attract females (Jukema and Piersma 2006). What makes them so interesting is that the males come in three polymorphs, each one genetically tied to a different courtship ritual (Jukema and Piersma 2006). Independent males are large and brown, displaying their plumage to potential mates and chasing away other independent males (Jukema and Piersma 2006). Satellite males are smaller, white, and unthreatening

(Jukema and Piersma 2006). Independent males tolerate satellite males in their territory, giving them the opportunity to quickly attempt copulations with the females also in the territory (Jukema and Piersma 2006). The final form of male ruffs are referred to as faeders, the smallest and most drab of the three (Jukema and Piersma 2006). Faeders mirror the plumage color and size of female ruffs and can freely move between independent males' territories (Jukema and Piersma 2006). In this way, they can attempt to sneak copulations from resident females (Jukema and Piersma 2006). In these examples, dishonest signaling is used to gain access to previously inaccessible females. While these behaviors are quite different than honest displays, their performers are nonetheless able to use their ornamentation and behaviors to mate with females, revealing them as unusual and fascinating forms of courtship rituals.

## Summary

Reproduction is one of the most important processes for animals, providing a mechanism to populate future generations and propagate species. Sexual selection results from individuals choosing mates based on the quality of certain preferred traits that are thought to provide benefits for either them, their offspring, or both. In order to advertise their traits and assess the quality of potential mates, many species have developed ornamentation and behaviors that serve as indicators of those traits. These are used in courtship rituals to attract mates, as well as serving other uses like defending territories and strengthening social bonds. Complex courtship rituals allow for more information to be signaled, and aspects of an individual's status such as health, genetic background, life experience, and social ranking can be communicated through courtship rituals. These accurate indicators of an individual's traits are called "honest" signals. Most courtship behaviors consist of honest signaling, but the presence of "dishonest" signals in some species reveal that not all courtship rituals are meant to signal quality. These deceptive signals are the exceptions, because they can only remain successful while

honest signaling is the norm. Whether it be through bright coloration, fighting, singing, dancing, gift giving, or any combination of physical attributes and behaviors, the ability to copulate with the opposite sex is vital for the survival of a species. The goal of identifying and courting a quality mate has led animals to develop the many wondrous and complex courtship rituals found in nature today.

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