Peacock Courtship

Britt Dahlin
Department of Biology
Lake Forest College
Lake Forest, Illinois 60045

Question: In a peacock's courtship display, how do iridescent feathers and shaking ("train-rattling") work together to catch a female's attention?

The glistening hues of a peacock's (Pavo cristatus) plumage have been a source of aesthetic and scientific recognition for years. Male peacocks, known for their brightly colored jewel-toned feathers, show off their colorful train or tail to attract a female. When it comes to selecting a mate, peahens (female peacocks) decide what is attractive. Peahens often choose males for the quality of their trains. There are a number of qualities that might contribute to the attractiveness of peacock plumage; wings, tail feathers, size, and the distribution of colorful eyespots may all play a role. Scientists continue to investigate what a peahen actually looks for in a mate's ornately feathered courtship displays, including how the iridescent feathers and shaking ("train-rattling") work together to catch a female's attention.

Broadly speaking, animals rely on various social cues transmitted during their interactions with potential mates. Mate choice directly affects an animal's reproductive fitness, and this process has generated a remarkable assortment of evolved traits and behaviors in many cases.

The peacock's magnificent tail is a well-documented example of the principle of evolution known as sexual selection. According to Charles Darwin, a biologist known for his contributions to the study of evolution, individuals best suited to survive will have more offspring than those that are less suited. This process, known as natural selection, is a key mechanism of evolution, and is also known as "the survival of the fittest" (Darwin 1859). However, some species have traits that seem to decrease their chances of survival. Darwin thought that features such as the peacock's train did not support his theory of evolution by natural selection; he believed that such an elaborate feature could be a disadvantage because it was burdensome in the face of predation. The long, heavy train does indeed make it difficult for peacocks to escape predators. The mysterious origin of the peacock's spectacular tail bothered Darwin, who wrote in 1859, "the sight of a feather in a peacock's tail…makes me sick!" (Darwin 1859). The peacock's tail did not evolve for natural survival; instead, the plumage resulted from the mating choices made by peahens. Darwin (1871) speculated that the peacock evolved its exotic tail to attract a mate, thus helping it produce more offspring and increase the number of offspring with attractive tails. Conflicting research results about female choice makes the "peacock's tale" an interesting story.

The function of the elaborate iridescent train of peacocks has been the subject of much scientific research and debate. The peacock's train most likely evolved through selection either because of its importance in male-to-male competition for mates or because it attracts females. This paper will focus on the theory that peahens choose mates because they are attracted to the peacock's elaborate trains and the way the iridescent feathers and shaking ("train-rattling") work together to create an eye-catching or hypnotizing effect.

To test Darwin's idea that the male's elaborate tail could have evolved because choosy females preferred it, Marion Petrie and her colleagues examined the role of the male peacock's tail in mating rituals. They observed male mating behavior in leks, sites with several males who display in close proximity for the purpose of mating. Petrie and her team found that males who had the longest trains and the most eyespots were the most successful with females (Petrie et al. 1991). While they admit not knowing the definitive reason for these elaborate trains, they do propose some possibilities, including that the males who possess these preferential train characteristics are in good health, have high status, are parasite free, and have survived into old age. Thus, the desirable genes will pass from the males to their offspring. Such ornamentation unequivocally attracts the females.

Petrie and Halliday (1994) conducted an experimental test to determine the importance of the peacock's train in determining male mating success. They confirmed the causal effect of eyespots by showing that removing about 20 eyespots can alter a male's mating success. Despite solid evidence that females prefer male peacocks displaying more eyespots in their trains and evidence that eyespot number is often correlated with male mating success (Petrie et al. 1991, Petrie and Halliday 1994, Loyau et al. 2005), contradicting studies have reported conflicting evidence. One study by Takahashi et al. (2008) found no evidence that females preferred more ornamented males, which rebuts the previous peacock studies. Loyau et al. (2008) downplayed the importance of the study by Takashi et al. (2008), arguing that one study was not enough to discredit the concurrent findings of earlier studies.

Dakin and Montgomerie (2011) repeated Petrie and Halliday's (1994) eyespot removal experiment. Dakin and Montgomerie (2011), who studied the geometric arrangement of tail feathers and natural variation in the number of eyespots displayed during courtship, confirmed Petrie's (1994) report that removing a large number of the outermost eyespots from a male's train decreases his mating success compared to unmanipulated males. However, they did not find a significant effect on mating success. Dakin's (2011) study also supports arguments raised by Takahashi (2008). Females in Dakin's (2011) study did discriminate against males with very few eyespots; however, there were not enough males with few eyespots to detect this without experimental manipulation (removing a number of eyespots through cutting tails). Peacocks whose tails are clipped enough that it reduces the number of eyespots are less successful at mating. Males with very few eyespots in their tail feathers -- a measure of the size of the tail -- were unattractive to females, but males with more spots than average had no advantage. Dakin's study (2011) suggests that in most situations, females do not pick mates based on the number of eyespots on their trains, but that the trait could help to eliminate unfit males who are missing a lot of feathers. According to Dakin et al. (2011), characteristics such as color and pattern of a train may still attract females. They suggest that peacocks who keep their feathers might be the healthiest and fittest. Traits such as the number of eyespots are only a rough measure of tail quality.

While there has been some conflicting evidence of the influence of train-feather eyespots on the mating success of peacocks, there is clear evidence that peahens use a peacock's tail when selecting a mate. Jessica Yorzinski and her colleagues wanted to examine what exactly was catching the eye of the peahen (Yorzinski 2013). Yorzininski et al. used eye trackers consisting of two lightweight cameras attached to a helmet that looped over the peahen's beak to track her eye movements when a peacock tried to get her attention. The results showed that during a male's courtship display, a peahen's gaze mostly tracks the lower part of a male's train, virtually ignoring the top part of the train, his head, and his crest. Additionally, females spent little time looking at the eyespots. However, these researchers also found that the peahens did look at the male's eyespots when he was farther away and the lower part of his body was obscured; peahens are apparently interested in the peacock's upper tail if nothing else is visible and from a far distance. The eyespots appear to function to help call the female towards the male, but once she is close, the eyespots are unimportant. Up close, the peahen may be judging qualities that include dense lower feathers, lower eyespots, and legs. When the female is up close, the male begins his wing shaking and rattling. These traits and behaviors serve to attract and maintain the attention of the peahen. Yorzinski's study (2013) shows that the train is important, but it does not rule out the significance of the male's eyespots. When male peacocks wiggle their wings, peahens look at them more. Similarly, Dakin and her colleagues confirmed that eyespots play a crucial role in when a peahen screens for a mate (Dakin et al 2013). In Dakin's study (2013), the researchers demonstrated that hue and iridescence of a peacock's blue-green eyespots greatly influences mating success; placing stickers over a male peacock's iridescent eyespots caused mating success to drop to nearly zero. However, this study does not address why peacocks shake their feathers.

For years, the peacock's multicolored eyespot feathers have intrigued scientists. Eyespots have a purple-black center surrounded by concentric blue-green and bronze-gold regions (Dakin and Montgomerie 2013). These researchers wanted to investigate the influence of all three colors on male mating success. In an earlier study (2009), Dakin and Montgomerie investigated the importance of visual signaling in peacocks. They found that males oriented themselves at an angle of 45 degrees to the sun and used the sunlight to enhance the appearance of their iridescent eyespot feathers during "train-rattling" displays. Because

males display at 45 degrees to the right of the sun's azimuth with the female directly in front, the researchers investigated how colors would be illuminated at 30 degrees, 45 degrees, and 60 degrees to the right of the female observer. While structural coloration causes the iridescence of the peacock's hues, the different angles of the nanoparticles within the fibers in the feathers catch and reflect the sunlight to create iridescence. Dakin and Montgomerie (2009) learned that courting males were more likely to perform "train-rattling" displays when the female was on the sunny side of the male's erect train. They also found that in peacock courtship, the angle of 45 degrees relative to the sun allows males to enhance the appearance of the iridescent eyespot feathers. In their 2013 study, Dakin and Montgomerie learned that eyespot color accounted for almost half of the peacock mating success and that the iridescence of the blue-green eyespot is the most important eye color variable. The researchers also experimentally manipulated the eyespots on nine peacocks and reported that mating success plunged to zero, supporting the notion that peahens attend to eyespots. The bronze-gold eyespot and the purple-black eyespot have a minimal effect on mating. This research shows that peacocks that display eyespots with more iridescence achieve more mating (Dakin and Montgomerie 2013).

Other characteristics of the tail's colors and patterns are critical for peacocks' mate choice. Dakin and a group of interdisciplinary scientists (2016) discovered that peacocks pursue females by vibrating their trains, which creates shimmering iridescence and mechanical sound. Peacocks rattle or shake their feathers about 25 times per second, creating a rattling sound and an iridescent visual display to attract peahens' attention. Dakin et al. (2016) analyzed the biomechanics of peacock's "train-rattling" behavior using high-speed videos and studying individual peacock feathers in a lab. Strumming their tail feathers against the back of their train, peacocks produce vibrations similar to those in guitar strings, which look like sine waves. The vibrations have smooth repetitive oscillations and are continuous. Dakin et al. (2016) also learned that even though longer feathers are heavier, peacocks with longer feathers shake them at higher frequencies (faster), maybe working harder in an attempt to show off their strength to peahens. Despite all this shaking or "train-rattling" to create a glimmering, iridescent background, the eyespots at the ends of the tail remain almost perfectly still because of tiny hooks that lock the feathers together. This produces a hypnotic effect that lures females. It is possible that this motion influences how peahens perceive the eyespot colors that are important for mate choice. The results of this study differ from Darwin's 19th-century conclusion that peacocks rattle their feathers together and that the vibrations serves to only make noise because it does not add to the beauty of the plumage. In contrast to Darwin's theory, these results suggest the possibility that sexual selection -- a female's choice -- is shaped by both the biomechanical design of the eyespot feathers as well as the behaviors that produce visual and audio cues.

Courtship and sexual selection in peacocks is very complex, but it is an area of great interest -- one that has resulted in research focusing on the spectacular displays animals use to attract a mate. In male peacocks' courtship displays, discrepancies exist in the parameters that peahens use when selecting a mate. Initial studies indicate that the appearance of the male's train is used in female choice (Darwin 1871, Petrie et al. 1991, Loyau et al 2005), while recent experimental tests challenge the results of earlier studies (Dakin and Montgomerie 2011). The peacock's train is a complex structure, and the exact reason that the male's train and display are attractive to females is less clear. While there is some consensus as to what characteristics of the male peacock's train are most favored by females, there is less consensus as to why. Research only demonstrates that a male peacock's plumage and courtship behaviors influence their success at attracting and mating with females. Researchers need to continue to determine what exactly peahens see in this biomechanical exploit. Further investigation into what makes one male stand out from others is necessary. Future research could also focus on why the eyespot contains three-color patches if two of them serve no purpose, whether peahens use variation in audiovisual features to discriminate among mates, and how "train-rattling" factors into sexual selection.

References

Dakin, R. & Montgomerie, R. (2009). Peacocks Orient Their Courtship Displays Towards the Sun. Behavioral Ecology and Sociobiology, 63, 825-834. https:/doi.org/10.1007/s00265-009-0717-6

Dakin, R. & Montgomerie, R. (2011). Peahens Prefer Peacocks Displaying More Eyespots, but Rarely. Animal Behaviour, 82(1), 21-28. https://doi.org/10.1016/j.anbehav.2011.03.016

Dakin, R. & Montgomerie, R. (2013). Eye For An Eyespot: How Iridescent Plumage Ocelli Influence Peacock Mating Success. Behavioral Ecology, 24(5), https://doi.org/10.1093/beheco/art045

Dakin, R., McCrossan, O., Hare, J. F., Montgomerie, R., & Kane, S. A. (2016).Biomechanics of the Peacock's Display: How Feather Structure and Resonance Influence Multimodal Signaling. PLOS ONE, 11(4), 1-25. https://doi.org/10.1371/journal.pone.0152759

Darwin, C., (1859). On the Origins of Species. Retrieved from https://www.gutenberg.org/files/1228/1228-h/1228-h.htm

Darwin, C. (1871). The Descent of Man and Selection in Relation to Sex. Princeton, New Jersey : Princeton University Press.

Loyau, A. Jalme, M.S. & Sorci, G. (2005). Intra-and Intersexual Selection for Multiple Traits in the Peacock (Pavo cristatus). Ethology, 111, 810-820. http://dx.doi.org/10.1111/j.1439-0310.2005.01091.x

Petrie, M., Halliday, T. & Sanders, C. (1991). Peahens Prefer Peacocks with Elaborate Trains. Animal Behavior, 41(2), 323-331.DOI: 10.1016/S0003-3472(05)80484-1

Petrie, M. & Halliday, T. (1994). Experimental and Natural Changes in the Peacock's (Pavo cristatus) Train Can Affect Mating Success. Behavioral Biology and Sociobiology, 35(3), 213-217. https://doi.org/10.1007/BF00167962.

Takahashi, M., Arita, H., Hiraiwa-Hasegawa, M. & Hasegawa, T. (2008). Peahens Do Not Prefer Peacocks With More Elaborate Trains. Animal Behaviour, 75 (4), 1209-1219.https://doi.org/10/1016/j.anbehav2007.10.004/.

Yorzinski, J., Patricelli, G., Babcock, J., Pearson, J., & Platt, M. (2013). Through the Eyes: Selective Attention in Peahens During Courtship. The Journal of Experimental Biology. 216(16): 3035-3046. http://jeb.biologists.org/content/216/3035

Zi, J., Yu, X., Li, Y., Hu, X., Xu, C., Wang, X., Liu, X., & Fu, R. (2003). Coloration Strategies in Peacock Feathers. Proc Natl Acad Sci USA. 100(22): 12576-12578. www.pnas.org/cgi/doi/10.1073/pnas.2133313100