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Visual, Auditory, and Olfactory Sexual Selection Methods in Birds Inform Mate Choice by Serving as Indicators for Mate Quality

Sexual selection is a type of natural selection that favors individuals who have attributes that enhance their mating success (Singer, 2016). In birds, males usually show more elaborate ornamentation and other highly desirable sexual traits than females. Female choice exists primarily because females invest a large amount of energy in their offspring and produce a smaller number of gametes compared to males. Females rely on indicators of health, vitality, and intelligence to determine which males are ideal mates. There are numerous indicators of health and sexual desirability but some of the most important deal with the senses: sound, vision, and smell. Acoustic and visual cues are the most obvious. A walk outside usually reveals the plethora of variation in song and morphology of bird species. However, scientists have uncovered important olfactory signals that inform mating as well.

Acoustic signaling is used in many bird species, in fact, the category "songbird" was formed because of these frequent and unique acoustic signals. Although song can be used to assert territorial dominance, it is also used in mating as an indicator of individual fitness. A bird with a greater ability to perform their species song repertoire likely has superior intellectual capabilities. Although song performance has links to cognition, it also serves as a good indicator of superior survival skills. Periods of mating are often highly stressful, and the singer must not only meet their metabolic needs, but must expend energy on singing as well. A bird with a larger repertoire may be able to defend their territory better than a lousy singer. These factors are taken into consideration come mating time.

Shahla and Yahya (1996) showed that acoustic sexual selection played a large role in the Indian Peafowl. They demonstrated that there was a skewed distribution of matings towards a few males. Acoustic signals are one significant factor that lead to this skewed distribution. This study showed that males with calls consisting of more than five notes were more likely to mate than males with fewer than five notes, while there were no significant findings between call rate and mating success. Interestingly, males often learned elaborate vocalizations and repertoires from experience, meaning that elaborate mating calls come with increased age. The dependence on mating calls prevented fruitless matings with sub adults, because they did not produce any mating calls. It also prevented matings with males that did not have a well-established territory, because males with a recently-established territory produce mating calls far less than 5 notes in length. Since the complexity of mating calls was a factor of consideration for female birds, older and more experienced males seemed to have an advantage. Females likely chose mates with more life experience because they could show their success in the form of vocal knowledge gained over adult life. Females may have been choosing more vocally experienced males, but perhaps more importantly, they were searching for signs of intelligence.

Females are wise to look for superior singers. MacDougall-Shackleton et. al (2007) demonstrated that complex songs are linked to enhanced neural activity. They proved that the number of songs in a song sparrow's repertoire is constrained by the size of the song control nuclei. This means that the number of songs reflects the overall developmental success of the male in question. In addition to informing the female about the overall developmental success of the male, song size is also indicative of the amount of physiological stress the bird is experiencing. In the study, nutritionally stressed European Starlings had lower humoral immune responses and smaller song repertoires than their nourished counterparts. Birds with more songs tend to have more robust immune systems with a greater number of lymphocytes in relation to red blood cells. The cellular components of these birds were ready to mount an immune response. Increased repertoire also indicated whether the male had homozygous deleterious alleles; males that resulted from inbreeding had lower developmental stability and this caused a decrease in repertoire size (MacDougall-Shackleton et. al, 2007). However, an increased song size was related to an increase in neutral-locus genetic diversity (MacDougall-Shackleton et. al, 2007). This study stressed the correlation between large song repertoire size and increased immune response, developmental success, and genetic diversity. Clearly, repertoire size provided ample information about the genetics and life history of potential mates.

Many birds have songs that are specific to their species and serve as a form of behavioral speciation by informing matings. However, there are several birds that expand their repertoires beyond the boundaries of their species-specific calls. One such bird with a drastically expanded repertoire is the Superb Lyrebird. The Superb Lyrebird is endemic to Australia and can mimic the calls of twenty different bird species (Taylor, 2014). Furthermore, the Superb Lyrebird can replicate man-made sounds like the clicking of a camera shutter and the wind beats or beak claps of other bird species (Taylor, 2014). The birds have their own innate calls too, including "territorial" and "invitation display"(Taylor, 2014). While the invitation display can sound cacophonous with sounds such as "twanging, clicking, scissors-grinding, thudding, whirring, 'blick'-ing, galloping", the territorial vocalizations of the Superb Lyrebird are often described as melodious (Taylor 2014). The diversity of sounds produced by the Superb Lyrebird attest to the mental capacity of the singers and the experiential knowledge that they have gained in their lifetimes: two important indicators of fitness that the females will take into consideration when considering mates. However, unlike song sparrows, Superb Lyrebirds borrow from seemingly infinite sources to assert their fitness. Although song is an important mode of sexual selection in birds, visual indicators of fitness are also ubiquitous.

Visual signs of fitness speak volumes because they serve as an honest sign of fitness. A bird cannot mislead a potential mate with a false appearance, since the birds' physicality has been determined by its genetic makeup and life history and is not easily changeable. Moreover, many visual displays confer a handicap that must be compensated for by the individual. For example, male long tailed widow birds with long tail feathers are more highly desirable to females. The tail can create drag and can make it hard to fly away from potential danger (Andersson, 1982). However, the fact that this male bird could survive despite handicap attests to the superior fitness of this individual. Another example of how visual display can put an animal at risk is brightness. A bird with a brighter display is more eye catching and stands out from its environment far more than a dull colored bird, thus making it an easier target for predators. This is called the handicap principle. These two factors combined make visual signals of the utmost importance.

Visual appeal also increases the probability that a bird will be considered a "leader". A study by Griggio and Tóth (2011) found that male and female Free-Living Rock Sparrows with larger yellow patches were more likely to be "leaders" and are followed by more group-mates within their foraging groups. Yellow patch size was the single most important indicator of leadership while capacity for parental care, sex, and condition were largely unimportant (Griggio and Tóth 2011). Feather ornamentation and brightness are traits that depend on the carotenoid intake of the individual bird (McGraw, 2010). Carotenoids act positively on the physiology of birds that ingest them (McGraw, 2010). Carotenoids are often used in ornamental traits and they provide a lens into the health of a bird and the quality of nutrition that it has received over its lifespan (McGraw, 2010). Perhaps birds with larger yellow patches were considered "leaders" because their displays attested to their foraging ability. It makes sense that females would choose males that are adept at survival, not only in foraging groups but as mates, since the male possesses attributes that would make their offspring successful. Yet, accomplished foraging is not the only feature that is reflected in feather display.

Bright and impressive feather displays are correlated with decreased levels of infection. One study by Hamilton and Zuk (1982) uncovered a strong positive association between brightness, size, and low parasite levels in North American passerines. They found that resistance to parasites and diseases was related to individuals with certain characteristics whose full expression relied on overall health. These visual displays are usually bright pigmentation in the feathers or fur. In other words, the females were looking for males that showed genetic resistance to the protozoa and nematode being tested for. Another good indicator of resistance to invaders is skin pigmentation. If any feathers have been removed, females are often able to assess the health of a male based on the pigmentation of veins and arteries at the surface of the skin. Several species even go so far as inspecting the urine of a potential mate. Size was also a measure of decreased parasitism; of the birds caught and examined, the researchers found that protozoans affected larger birds less. One possible reason why this may be is because larger birds have a larger volume of blood and each bite subtracts a smaller fraction of total blood. Larger size also correlates with increased fighting ability and with increased showiness. Brightness and size were two reliable indicators of parasite and nematode resistance, two visually available signs that gave females insight into health of potential mates. But sometimes a bird's physical displays are subtler.

In a study by Alonso et al. (2014), the Great Bustard *Otis tarda* males displayed their cloaca for females to inspect and assess. Great Bustards eat Blister Beetles even though they contain a poisonous compound called cantharidin. However, even though cantharidin is toxic at moderate dosages, eating cantharidin can protect the Great Bustards in significant ways. Cantharidin is known to have anthelminthic properties and to eliminate gastrointestinal bacteria that cause sexually transmitted diseases. Both sexes consume cantharidin come mating time. However, males eat larger blister beetles and more of them, which increases their cantharidin consumption compared to females. This increases their sexual appeal and makes them appear more vigorous because it eliminates infections of the cloaca. Female Great Bustards carefully survey the cloaca of potential mates. Females look for mates with cloacas that are free from infection, clean, and white. Females can glean two important pieces of information from a spotless cloaca: that the male is resistant to cantharidin and that the male is parasite free. The absence of sexually transmitted disease will not only keep the female great bustard in good health but also increase the chance that her offspring will inherit cantharidin resistance and be successful in managing parasites. This visual display is far less obvious compared to plumage, but a clean cloaca can provide ample information about resistance and sexual health so it should not be discounted as an example of visual sexual selection. Although visual signals are informative sometimes the best way to exchange information is through scent.

Olfactory signaling appears to have important implications in bird mating. Up to the fourth quarter of the 20th century, the olfactory machinery of birds was not well studied (Balthazart and Caro, 2012). Birds were presumed to be anosmic or microsmatic (Balthazart and Caro, 2012). Visual and acoustic modes of sexual selection in birds were so obvious and prolific in the natural world that many scientists simply thought that olfaction would be unnecessary for birds (Balthazart and Caro, 2012). Birds can see UV light and nearly every species had their own song or mating ritual, so biologists wondered why they need the added power of an olfactory information stream. However, Bang and Cobb launched the investigation into avian olfactory faculties with research that examined avian olfactory bulbs and compared olfactory machinery and size between different species of birds (Bang, 1960) (Bang and Cobb, 1968). This groundbreaking research provided the first morphological evidence of bird's sense of smell. After this initial breakthrough, investigators kept on making key discoveries, expanding knowledge of avian olfaction. They found that groups of birds such as ducks, auklets, and petrels produce species specific scents that have consequences in social interactions such as increasing neural activity during mating (Balthazart and Caro, 2012). There is a growing body of research that demonstrates the multitude of ways in which smell informs bird's social behaviors, yet an indisputable pheromone has yet to be identified (Balthazart and Caro, 2012). Still, many experiments have proved that birds can distinguish between avian odors from different sources.

In some birds, glands secrete substances that provide information. Most birds have a uropygial gland that secretes preen oil (Atwell et al. 2011). Preen oil consists of volatile compounds that act like pheromones by conveying specific qualities of individual birds (Atwell et al. 2011). Research has shown that seabirds and parrots use intraspecific chemical communication, but passerine songbirds were categorized as the birds least likely to use chemical signaling (Atwell et al. 2011). Until Atwell et al. (2011), no one had studied whether passerines could distinguish among individuals based on the composition of their preen oil. Within the study, Atwell et al. tested if Dark-Eyed Juncos could distinguish between preen oils from members of their own species vs. other species, male and female Dark-Eyed Juncos, Dark-

Eyed Juncos from the same population vs others, and males with large vs small ornamentation (2011).

They found that both males and females spent more time examining preen oil from male birds (Atwell et al. 2011). This suggests that males investigated the preen oil of other males over females because of the impulse to fend off potential rivals and defend their territory as a territorial monogamous bird (Atwell et al. 2011). The Dark-Eyed Juncos could distinguish between conspecifics and heterospecifics and male and female conspecifics. However, it was not clear if the birds could not distinguish between conspecifics from the same or different population, or between males with large or small plumage ornaments (Atwell et al. 2011). Curiously, females seemed to spend more time with the preen oil of smaller males whose oil contained less masculine characteristics (Atwell et al. 2011). Two interpretations of these results offered by the authors are that females are actively avoiding strong "male" scents because of their correlation with aggression, or that females are choosing scents that are less masculine because of desirable phenotypes tied to femininity. Either way, the Dark-Eyed Juncos are gaining important information from preen oil about the species, sex, size, and maybe even how aggressive the individual is. These inputs can be synthesized so that the female chooses a good candidate for mating.

Some birds have mating rituals that allow for scent exchange. Crested Auklets perform a repetitive courtship behavior known as the "ruff sniff" that allows potential pairs to gather olfactory information about one another (Hagelin, 2003). The Auklets employs a unique scent reminiscent of tangerine to evaluate mates (Hagelin, 2003). This tangerine scented oil is concentrated around the nape so one bird will rub its bill in the nape feathers of the other display partner (Hagelin, 2003). The tangerine scented plumage odor is heightened during breeding season and contains two chemicals that primarily influence social behavior: *cis*-4-decenal and octanal (Hagelin, 2003). The authors used a T-maze to test whether auklets preferred conspecific scents and responded differentially to certain scents (Hagelin, 2003).

Auklets preferred the fresh plumage odor of breeding Auklets to the unscented plumage of a Parakeet Auklet, indicating that scent was a significant lure (Hagelin, 2003). The researchers showed that Auklets preferred tangerine aldehydes over natural plumage oil, suggesting that there are key chemicals within the oil that elicit behavioral responses (Hagelin, 2003). Additionally, when the concentrations of these chemicals increase, the corresponding response generated by the Auklet also increases (Hagelin, 2003). Moreover, Auklets showed an aversion to mammalian musk and were apathetic to banana essence (amyl acetate), further strengthening the conclusion that only certain conspecific scents produce a positive response or a response at all (Hagelin, 2003). Novel scents like sweet banana essence evoked no response because they have not been encountered before and thus are viewed as neutral (Hagelin, 2003). Not surprisingly, scents like mammalian musk do not elicit a positive response, but a negative response (Hagelin, 2003). Two possible reasons why mammalian musk is avoided is because it may be indicative of a predator or simply unpleasant to Auklets (Hagelin, 2003). This study was important because it shows that plumage oil contains specific chemicals that serve as mate quality indicators. Furthermore, it illustrates that behavioral rituals can aid in the passage of olfactory cues and that scent is not only used in mating but possibly for predation and defense.

In some cases, olfactory stimuli and machinery lead to certain key sexual behaviors. Male Mallard Ducks form groups of 4-10 at the end of Summer extending into the beginning of Fall (Balthazart and Taziaux, 2009). Once in a group, they exhibit behaviors such as head-up-tail-up, head-down-tail-up, and grunt whistles (Balthazart and Taziaux, 2009). They perform these social displays from September to February to other groups of males as a form of competition and to females as a mode of attraction (Balthazart and Taziaux, 2009). Once a male has succeeding in attracting a female they will form a pair and copulate. Balthazart and Taziaux (2009) were interested in seeing if olfaction was responsible for these behaviors. They sectioned the olfactory nerves of select mallard duck males and observed their behaviors over the duration of Winter (Balthazart and Taziaux, 2009). They found that these ducks did not show key behaviors associated with mating like mounting, latching onto the female's neck feathers, and even copulating. Birds in a control group that had undergone a sham surgery, which did not interfere with the olfactory nerve, did not show a decline in mating behaviors. One of the most likely reasons for the decline in sexual behaviors in the birds with the actual surgery was that olfactory information from sexual partners could not be integrated by the male bird. Another possible reason is retrograde degeneration of the olfactory bulbs (Balthazart and Taziaux, 2009). Since the olfactory bulbs are implicated in controlling the strength of behavioral responses in addition to receiving olfactory stimuli, degeneration could decrease behaviors (Balthazart and Taziaux, 2009). This experiment further substantiates the large impact of olfactory cues and machinery in sexual behaviors. Not only is the olfactory nerve important for reception of stimuli, but also to upregulate and downregulate key behavioral responses.

Sexual selection favors individuals with attributes that better their mating success (Singer, 2016). Olfactory, visual, and acoustic cues are signs of male fitness and inform females about positive or negative qualities that potential mates possess. Olfactory cues can provide females with information about the size, species, sex, and even behavior of other birds. Visual cues give females information about the developmental success, nutrition, foraging ability, and genetic quality, while acoustic signals allow females to access the intelligence of males. These three modes of sensory sexual selection inform females, and heavily influencing mate choice. It will be interesting to learn about future discoveries regarding how birds sense the world around them and use this to make important mating choices. It will be especially interesting to see if future discoveries in avian olfaction identify verifiable avian pheromones that are important in sexual selection.

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