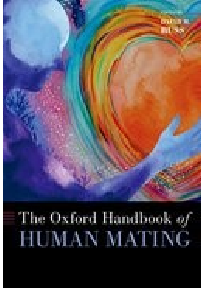

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CHAPTER

2 Sexual Selection and the Animal's Mating Mind

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Abstract

Moving from Darwin's theory of natural selection, I briefly review his theory of sexual selection and focus on his idea of female mate choice and the sexual aesthetics that motivate it. I review some early hypotheses on the adaptive significance of mate choice. Going forward, I then introduce studies that attempt to uncover the underlying mechanisms that define a female's sexual aesthetics. Much of evolutionary psychology has been derived from basic notions in evolutionary biology, especially in mate choice. Here, I turn the tables and review studies of animal mate preferences that have been inspired by studies of humans in the fields of psychophysics, behavioral economics, and neuroaesthetics.

Keywords: sexual selection, mate choice, psychophysics, sexual beauty, irrational choice

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Sexual Selection Theory

It has been 150 years since the publication of *The Descent of Man and Selection in Relation to Sex* (Darwin 1871), and a bit longer since Charles Darwin exclaimed, "… the sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" (Darwin 1860). Darwin already had one important theory, natural selection, under his belt when he turned his attention to what initially seemed to be a contradictory theory, sexual selection.

Darwin had an aversive reaction to the peacock's tail because the mere existence of this ornament seemed to run counter to predictions of natural selection, the evolution of traits that enhance survivorship. The peacock's tail is not an isolated example. Elaborate traits that seem to compromise survivorship are found throughout the animal kingdom among most sexually reproducing taxa, and these ornaments are perceived in all sensory modalities. These types of traits include birdsong, cricket and frog calls, firefly flashes, brilliant colors of many fish, and the musty odors of many mammals. These traits share other attributes: they are involved in mating behavior and they are sexually dimorphic, often being more extensively developed in males than in females.

In retrospect, Darwin's sexual selection hypothesis does not seem complex. Like natural selection, evolution by sexual selection requires variation, selection, and inheritance. The ↳ difference is in the second step. Natural selection favors those variants with higher survivorship while sexual selection favors those variants with greater mating success. Darwin suggested that sexual selection favored two types of traits: those that enhanced an individual's access to members of the other sex and traits that made courters more attractive to members of the opposite sex, the choosers; in short, armaments and ornaments. An important caveat is that there is substantial variation in the animal kingdom, and there are cases in which females exhibit the more elaborate courtship traits and other species, such as our own, in which males and females both exhibit these types of traits (Rosenthal 2017). Nevertheless, Darwin posited that in most animal mating systems, males are competing for either access to or the attention of females.

Male-male competition was not a controversial idea perhaps for several reasons (Richards 2017; Ryan 2021). Males battling for access to females did not seem all that different from activities favored by natural selection and conformed to Tennyson's epitaph that nature was "red in tooth and claw." The idea of mate choice, however, rankled many of Darwin's supporters, especially Alfred Russel Wallace. Many of Darwin's contemporaries had a hard time empowering female animals as the agents who decide who gets to mate, and they also found Darwin's explanation of why females have these preferences, that they were grounded in the female's sexual aesthetics, as rather wanting. Darwin's theory laid mostly fallow for about a century (Richards 2017; Ryan 2021).

There was a resurgence of interest in sexual selection by mate choice one hundred years later that resulted in large part from Campbell's edited book *Sexual Selection and the Descent of Man, 1871–1971* (Campbell 1972), and especially Trivers's (1972) chapter on parental investment and sexual selection. Trivers was influenced by the early work of Bateman (1948), who showed that in fruit flies the number of matings had a larger effect on male reproductive success than on female reproductive success. Trivers pointed out that this discrepancy arises from greater female investment in her gametes than male investment in his gametes. This gives rise to a sexual conflict of interest (Arnqvist and Rowe 2005) in which males should be under selection to mate often and females should be under selection to mate carefully. A point sometimes overlooked by critics in the social sciences is that this formulation firmly planted females in the driver's seat; they were the deciders. But when Darwin moved on to discuss humans, he returned to a more Victorian view of the sexes (Richards 2017).

Bateman's principle, as it is now called, has been productively criticized on a number of fronts (Gowaty et al. 2012; Tang-Martínez 2016). A recent meta-analysis of a large number of mating systems, however, upheld Bateman's and Trivers's prediction of these sex differences in mating roles (Janicke et al, 2016). In addition, Borgerhoff Mulder and Ross (2019) critically and carefully applied Bateman's principle to their analyses of twenty years of data on marriage systems of the Pimbwe in East Africa.

Darwin's theory of sexual selection by mate choice has attracted more attention and consternation than his theory about male competition for access to females. It was much ↳ easier to explain the evolution of armaments than ornaments. Post-Trivers, behavioral ecologists showed that in many cases female mate choice garnered resources that increased her reproductive success. But the question that seemed to most interest behavioral ecologists was what kind of information about the male's genetic quality is communicated to the choosing females. The good gene's hypothesis posits that males advertise genes that enhance survivorship, and females are under selection to choose these males because of the genetic benefits to their offspring (Hamilton and Zuk 1982; Rowe and Houle 1996; Zahavi 1975). Theory suggests this hypothesis is logical (Grafen 1990), but there is not overwhelming empirical support that it is biological. Surely, good genes selection occurs, but estimates of its relative effect in nature are relatively small (Achorn and Rosenthal 2020; Kirkpatrick and Barton 1997; Møller and Alatalo 1999; Rosenthal 2017).

More recently, research in the realm of sensory ecology, neuroethology, and neuroscience have shown how selection on sensory, neural, and cognitive systems in other domains can have important influences on what females find sexually beautiful. These studies are providing important insights into the scaffolding of an animal's sexual aesthetics. This is the line of research I follow in the remainder of this chapter.

Sexual Selection and Evolutionary Psychology

Evolutionary biologists have long been interested in human biology, and especially human behavior. Darwin is a prime example (Darwin 1871, 1872). Much of the current interest in the evolutionary basis of human behavior probably has its roots in *Sociobiology* (Wilson 1975). That book, and especially the last chapter, "Man: From Sociobiology to Sociology," both garnered the most criticism from the general audience and also provided the foundation for evolutionary psychology. Many of the subjects in evolutionary psychology (e.g., altruism, mutualism, war, and sex) address ideas that populated that chapter (Barkow et al. 1992; Buss 1994; Miller 2011). Thus it seems fair to say that evolutionary biology writ large has inspired much of what is going on today in evolutionary psychology.

I am going to turn the tables. I am going to review a number of recent avenues of interest in animal sexual selection and mate choice that are inspired by studies of humans, especially in the fields of psychophysics, behavioral economics, and neuroaesthetics.

Cognitive Aspects of Mate Choice

A number of researchers working parallel to or collaborating with behavioral ecologists have delved into the neural underpinnings of female preferences. What is it about the female's brain that makes her perceive some traits as more attractive than others? In a variety of taxa and in all sensory modalities, researchers have uncovered neural biases at the sensory periphery and neural circuits in the brain that contribute to the female's sexual aesthetics (e.g., Endler 1992; Gerhardt and Huber 2002; Greenfield 2002; Wilczynski and Ryan 2010).

Although these studies in neuroscience have provided unparalleled understanding of the neural scaffolding of the female's sexual aesthetics, another set of questions concerns the cognitive aspects of mating decisions. By the animal's cognitive processes we refer to Shettleworth (1998), who defines cognition as the acquisition and analysis of information in the environment that contributes to decision-making. I will review a number of studies, including several that we conducted with túngara frogs, that were inspired by studies of human behavior.

Weber's Law

We know from the notion of the *Umwelt* by von Uexküll (1982; see also Caves et al. 2019) that different animals perceive the environment in different ways. This is obvious when we compare the sensory limitations of ourselves to other animals. For example, we cannot hear the ultrasonic echolocation calls of bats nor the infrasound of elephants; we cannot see in the ultraviolet as can bees, fish, and birds, nor can we sense infrared with the precision of a rattlesnake. We cannot share the olfactory experiences of man's best friend and are unable to sense the signals of most electric fish.

Another limitation is how we compare stimuli within a range we can sense. Psychophysics is a field with a long and distinguished history that is concerned with how we translate stimuli into perception. Many studies show that humans, and other animals as well, do not compare stimulus intensities as they actually exist; our perceived difference between stimuli is often not based on absolute (linear) differences but on proportional ones. These studies are often done in the context of just noticeable differences (JNDs): the minimum difference between two stimuli for us to perceive them as different. Akre and Johnsen (2014) reviewed a number of studies in humans (as well as other animals) showing proportional comparisons in different sensory modalities: in hearing in terms of amplitude and frequency comparisons; in vision in terms of comparisons of area, intensity, and wavelength; in temporal duration in both auditory and visual domains; and in our number sense (see also Shepard 1987).

Although there are exceptions, many of these comparisons follows Weber's law, which is $\Delta I = kI$, where ΔI is the JND, the magnitude of the stimulus is I and k is a constant. What is clear from this equation is that as stimuli become larger in magnitude, their differences must be greater for us to be able to detect differences between them. In the context of animal behavior in the wild, we are more concerned with just meaningful difference (JMDs; Nelson and Marler 1990) than JNDs.

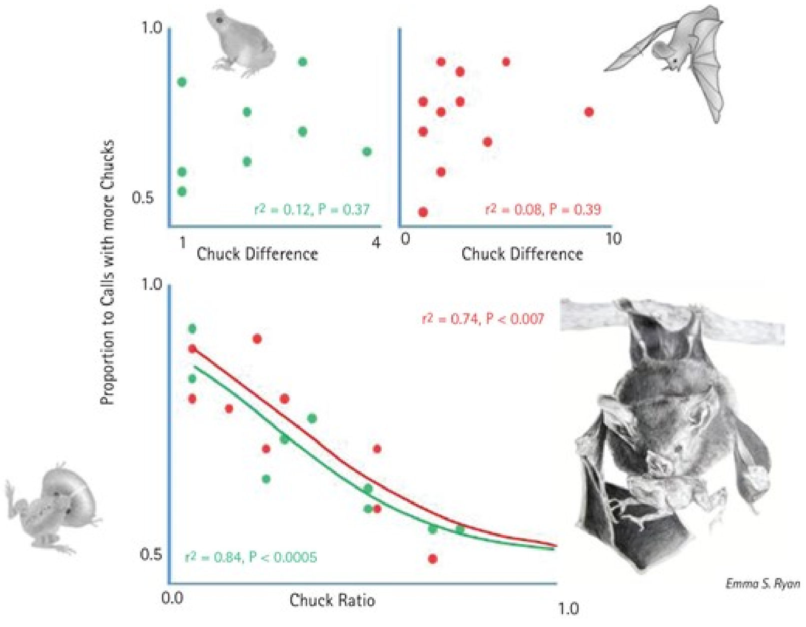
Mate choice is all about comparisons whether it is between two or more individuals or one individual and a neural template; it is of some importance that we understand how these comparisons are made. In 1984, Cohen (1984) asked if these female comparisons followed Weber's law; it took more than twenty-five years to get an answer.

Túngara frogs have become a useful system for asking questions about sexual selection and communication. p. 20 As I refer to this system several times, it is worthwhile to summarize ↳ the mating system (Ryan 1985, 2011). These frogs breed during the rainy season in much of the New World Tropics. Males gather in choruses and call for females. Females choose the males with whom they want to mate, the male and the female construct a foam nest with about two hundred fifty eggs that hatch within a few days. There is no parental care of the eggs once the nest is constructed. As with most frogs, the female's mate choice is based primarily on the male's call. The call contains two components, a whine which may or may not be followed by chucks. The whine is necessary and sufficient to attract females for mating, but the addition of even a single chuck, they can add up to seven, increases a male's attractiveness to the female fivefold. Females also tend to prefer more chucks to fewer chucks. Despite the sexual potency of chucks, males only add chucks when vocally competing with other males, even though all males are capable of producing chucks. The benefit of adding chucks is countered by the frog-eating bat. They are attracted to the male's mating call and like the female frogs are about five times more attracted to calls with chucks than calls without chucks; the difference being that females are searching for a mate while the bats are searching for a meal.

Females prefer more chucks to fewer chucks, but how is that comparison made, are they comparing absolute numbers of chucks or is the comparison proportional? If they are following Weber's law, we would predict, for example, that the strength of preference for six chucks versus five chucks would be less than the strength of preference for two chucks versus one chuck. If, on the other hand, they are comparing absolute chuck number, then the strength of preference should be the same. Akre et al. (2011) tested female frogs in two-choice phonotaxis tests in which the two stimuli had the same whine but varied in the number of chucks. The strength of preference was estimated by the proportion of females that preferred the call with more chucks. Proportional differences in the number of chucks explained significantly more of the variation in the strength of preference than did the absolute differences in the numbers of chucks (84 percent vs. 12 percent; fig. 2.1).

Are proportional comparisons an adaptive strategy for mate choice in túngara frogs, or is this just the way that many brains make comparisons? If the latter is the case, we might expect frog-eating bats to also follow a Weber-like function when comparing chuck number. Analogous choice experiments conducted with the bats with the same call stimuli revealed strikingly similar results: proportional differences in the number of chucks explained 74 percent of the variation in the strength of preference while absolute differences in chuck number explained only 8 percent of the variation in the strength of preference (fig. 2.1). These results can have important consequences for how sexual selection proceeds. They suggest that as a sexual trait increases in magnitude, a peacock's tail for instance, a male must be absolutely more and more different than his competitors to be perceived as more attractive. We know that natural selection is an important counterselection force on the evolution of elaborate male courtship traits (Kirkpatrick and Ryan p. 21 1991), but this study suggests there is also a cognitive brake on the evolution of exaggeration. ↳

Figure 2.1



The proportion of female túngara frogs (green) and frog-eating bats (red) that preferred the call with more chucks as a function of the difference in the number of chucks being broadcast from each speaker (top) or the ratio of chuck number being broadcast from each speaker (bottom).

Although it has long been known that humans often follow Weber's law when comparing stimulus magnitude (see above), Gassen et al. (2022) recently showed proportional comparisons when humans compare facial attractiveness. They used morphing software to generate faces that varied between photos that were prerated as below and above average in attractiveness. The results revealed that the judges were making proportional comparisons, images for the more attractive faces had to be more different quantitatively to be perceived as more attractive. These results were also consistent with simultaneous eye-tracking data.

Spatial Illusions

Holding distance constant, we see larger objects as larger than smaller ones because they subtend a greater angle of the retina. Holding size constant, we perceive closer objects as closer for the same reason. But we are usually able to parse the effects of size and distance due to what has been called size–distance invariance. Although vision researchers still do not understand exactly how this happens, we know that the invariance phenomenon is not all that invariant (Kim et al. 2016). But we also know that we don't get fooled p. 22 into thinking that the coffee cup in front of us is larger than a more distant building. ↳ Filmmakers, photographers, and architects have been able to exploit this size–distance phenomenon in a myriad of applications.

When we view a building with several floors we implicitly assume that the exterior windows are all the same size even though the windows on higher floors appear smaller. The perceived size difference between the windows on the ground floor and the top floor gives us an estimate of the height of the building. Cinderella's Castle at Walt Disney's Magic Kingdom creates a perceptual illusion by toying with our size–distance relationships. The castle windows in the upper floors are absolutely smaller than the windows on the ground floor. We do not know that when we look at the castle, and thus the castle appears taller to us than it actually is (Ryan 2018).

We know that animals have evolved a variety of patterns to manipulate the perceptions of their predators to afford themselves a modicum of safety (Stevens and Merilaita 2009). Greater Bower birds exploit perceptual biases in the mating domain. Males construct a bower; its function is to provide an arena in which males display to females standing in an avenue that leads up to the bower. The males decorate the avenue with a variety of objects, such as stones and shells. But they do not do so in a haphazard manner. The larger objects are placed closer to the bower and the smaller objects farther away. This creates a forced perspective the opposite of the Cinderella Castle, the bower appears smaller than it actually is. Endler and his colleagues suggested that the male courting in the bower now appears larger and thus more attractive to the female

(Endler et al. 2010). Data on male mating success collected in the wild supports their hypothesis (Kelley and Endler 2012).

Auditory Illusions

Studies of two auditory illusions have inspired some studies of mate choice in túngara frogs. The first is the McGurk effect, which is described as “hearing lips and seeing voices” (McGurk and MacDonald 1976). In these experiments, the sound of a phoneme is morphed onto a video of lips speaking a different phoneme. Amazingly, the observer perceives a third phoneme. For example, the sound of /ba-ba/ is morphed onto the video of lips speaking /ga-ga/; instead of perceiving either of these two phonemes, the observer instead perceives /da-da/. These studies show that auditory and visual stimuli, and probably other multimodal stimuli, are not perceived as individual elements but as an integrated whole.

Another auditory illusion is referred to as auditory continuity (Bregman 1994). Researchers present the observer a pure tone with a silent gap in the middle. Observers clearly perceive the two separate segments of the tone. They then added white noise to the gap and increased the amplitude of the white noise until the observer hears a continuous tone. This study shows how auditory perception can fill in gaps with meaningful stimuli, much as our visual system fills in blind spots (Pessoa et al. 1998).

Like most frogs, túngara frogs have vocal sacs that inflate and deflate synchronously with the call. The vocal sac increases the visual conspicuousness of the calling male and p. 23 ↳ it also influences the female’s mate choice. She is more attracted to a standard call (e.g., a whine-chuck) that is paired with an inflating vocal sac of a robo-frog compared to the same call by itself (Taylor and Ryan 2013; fig. 2.2). As with the McGurk effect, the temporal relationship between the call and the vocal sac influences the female’s perception. If the vocal sac is inflated after the call, then the visual cue does not enhance the call’s attractiveness; in fact, it makes it less attractive (fig. 2.2). Temporal relationships of the acoustic call components also influence the saliency of the acoustic signal. In a normal call, the chuck immediately follows the whine, which is about 300 ms from the beginning of the whine. If the chuck is displaced so that it is now 500 ms from the initiation of the whine, the chuck no longer increases the attractiveness of the whine (fig. 2.2). If these two unattractive signals are combined, a whine followed immediately by the vocal sac inflation and the 500 ms-displaced chuck, this unnatural multimodal signal is as attractive as a standard whine chuck (fig. 2.2). The interpretation is that the presence of the vocal sac perceptually rescues the displaced chuck; that is, it creates a multisensory illusion in the female so that she now perceptually binds these three components into a single perceptual unit (Taylor and Ryan 2013). This is especially interesting because these frogs did not exhibit auditory continuity in manipulations of the whine (Baugh et al. 2016) or when white noise was produced between the whine and the temporally displaced chuck (R. Taylor, unpublished data).

Mate Choice Copying

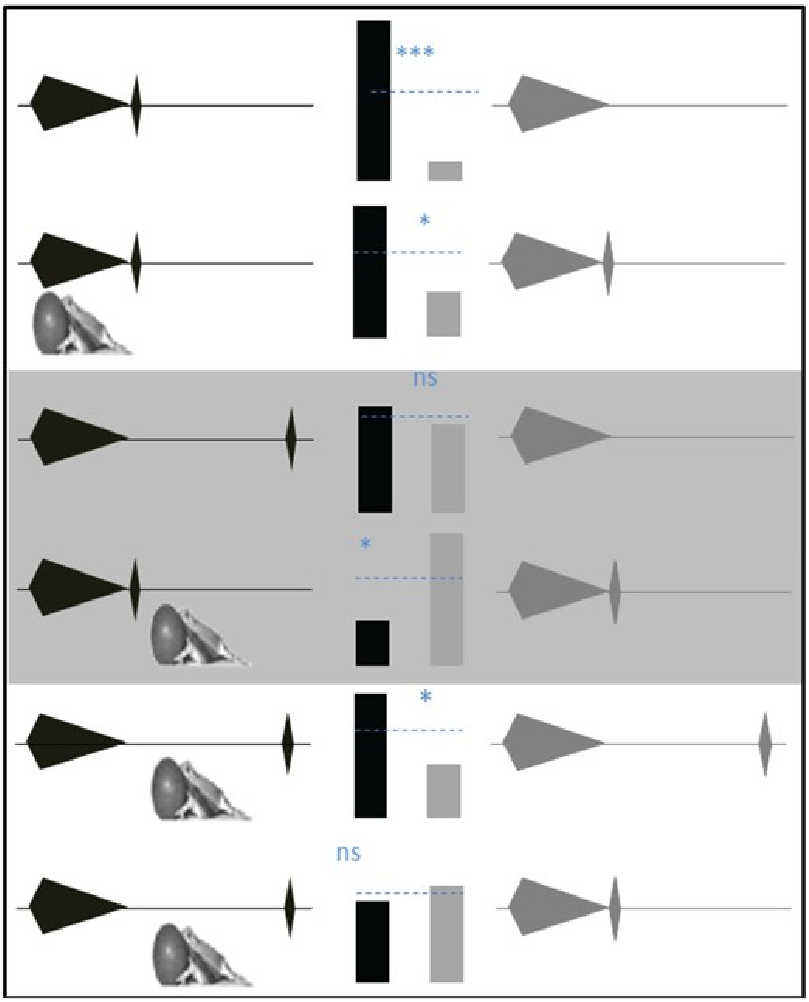
Before mate choice copying was a thing, psychologists had shown that social perceptions of a man could be influenced by the attractiveness of a female consort. The experiment was quite simple (Sigall and Landy 1973). A subject entered a waiting room where there was already one man and one woman. The man was of average attractiveness and the woman was judged as either attractive or unattractive. The subject was asked to rate the degree to which they might like or dislike the man; the subjects rated the man with the more attractive woman as more likable. Even though this study was not specifically addressing sexual attractiveness, it clearly shows that the halo cast by the woman was dependent on her attractiveness. Numerous other studies have shown similar effects in humans in the context of mate choice copying (Hill and Buss 2008).

Studies of mate choice copying in animals became a widely studied phenomenon after Dugatkin’s pioneering studies of guppies. Guppies are quite variably colored fish and a number of studies have shown that females prefer males with more orange (Houde 1997). Dugatkin (1992) conducted a simple experiment that quickly became a standard for animal mate choice studies. A focal female was placed in an aquarium in which there was a male on each side separated from the focal female by a pane of glass. The female could freely move within the aquarium and be courted by each male on the other side of the glass divider. As had been shown in previous experiments, the focal female spent more time courting the male with more orange.
p. 24 The focal female was then moved back to ↳
p. 25

↳

the middle of the aquarium and constrained inside a glass cylinder. A live “model” female guppy was placed with the less preferred male and the focal female could observe the two interacting. The model female was removed, the choice test was repeated, and the focal female now switched her preference to the previously less preferred male. The interpretation was that the perceived attractiveness of the male increased once he was observed courting another female.

Figure 2.2



Results of phonotaxis experiments between the stimulus on the left (black) and the stimulus on the right (gray). Black bars represent the proportion of responses to the black stimulus, gray bars represent the proportion of responses to the gray stimulus. The image of the robo-frog indicates the presence and temporal occurrence of the visual stimulus, an inflating–deflating vocal sac. In the top panel: females prefer a whine-chuck to a whine, and they prefer a whine-chuck associated with an inflating vocal sac versus a whine-chuck with no visual stimulus. In the middle panel: females did not discriminate between a whine with a silent gap followed by a chuck versus a whine only, while the females preferred a whine-chuck to a whine-chuck associated with the visual stimulus when vocal sac inflation occurred at the end rather than at the beginning of the call. In the bottom panel: females preferred a whine followed by an inflating vocal sac followed by a chuck compared to the same call without the visual stimulus; the whine–vocal sac inflation–chuck was as attractive as a normal whine-chuck. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

A mate choice copying study helped resolve a conundrum in another species of fish. The sailfin molly is found from coastal central Mexico around the Gulf of Mexico and up the eastern seaboard of the United States to the Carolinas. Like most fish, they reproduce sexually. The Amazon molly, however, is an all-female species that reproduces clonally; however, females must acquire sperm to trigger development of their clonal eggs, there is no fertilization. One of the species they mate with is the sailfin molly. The association between the sexual and asexual species raises a number of questions, one of which is—why would a male sailfin molly mate with an Amazon molly since the mating will not contribute to his reproductive success? It was thought that males might not be able to discriminate between their own females and Amazon females, but that is not true. Even in areas where Amazons do not occur, male sailfins prefer females of their own species over Amazon females (Gabor and Ryan 2001; Ryan et al. 1996). A mate choice copying experiment similar to the one conducted with guppies by Dugatkin suggested an answer. A focal sailfin female was given a choice between two male sailfins and predictably she preferred the larger male. In this experiment, a model Amazon female was added to each of the chambers with a male, but the focal sailfin female could only see the less preferred male interacting with the Amazon, her vision of the model Amazon with the preferred male was blocked so she could only see the male. The choice experiment was repeated and, as with the guppies, the female sailfin spent significantly more time with the smaller male whom she had just observed courting an Amazon (Schlup et al. 1994). The same experiment was later replicated in the field (Witte and Ryan 2002). The interpretation is that even though males do not accrue an immediate reproductive benefit by mating with Amazons, their attractiveness in the eyes of their own females, and supposedly their future reproductive success increases.

Hill and Ryan (2006) then asked if the attractiveness of the model influences the degree of mate copying, much as the attractiveness of a female consort influenced the likability of her male associate in the human study discussed above. Also as noted above, male sailfins can discriminate between female sailfins and Amazons and prefer to court their own species. In the eyes of males, female sailfins are higher-quality mates than Amazons. Female sailfins can also discriminate between female sailfins and Amazons.

The researchers conducted similar mate copying studies just described but with a twist. After the initial choice the less preferred male was paired with a female sailfin while the preferred male was paired with an Amazon female. The focal female was able to observe each of these males courting his model female, the model females were then removed and ↳ the choice test repeated. Focal females significantly increased their time associating with the previously unpreferred male who had just been courting a high-quality female and decreased the amount of time spent courting the previously preferred male who had just been observed courting a lesser-quality female. Thus, not only does the presence of the female influence a male’s attractiveness, but the female’s attractiveness itself influences the male’s attractiveness.

Mate choice copying has been demonstrated in numerous animals, not just in fish, and there have been a number of suggestions as to why it is adaptive for females to exhibit mate choice copying. Less attention has been given to the hypothesis that mate choice copying is just one manifestation of a more domain-general type of social facilitation (Westneat et al. 2000). As I argued that following a Weber-like function in comparing mates is not an adaptation for mate choice per se in túngara frogs, the same might be true in mate choice copying. There is some evidence for this idea in humans. Heterosexual women viewed photographs of men’s faces on a computer screen, received feedback in real time as to the ratings given by other subjects, and were then able to change their rating. The results showed that subjects changed their rating of facial attractiveness in response to feedback from others. For every 1.0 point difference from the feedback score, the subject changed her rating by 0.13 points. The magnitude of this effect, however, was similar in an analogous experiment that rated the attractiveness of hands, a change of 0.13, and abstract art, a change of 0.14. Their conclusion was that mate choice copying in humans might be one expression of a broader domain-general social facilitation and not necessarily an adaptation for mate choice per se (Street et al. 2018).

Closing Time

In 1979, Pennebaker et al. (1979) published an interesting paper under the title *Don’t the Girls’ Get Prettier at Closing Time: A Country and Western Application to Psychology*. This study was inspired by the lyrics of the song by Mickey Gilley, which suggested the perceived attractiveness of other-sex patrons in a bar increases as closing time approaches. Their data supported Gilley’s narrative. For both men and women, the attractiveness of opposite-sex but not same-sex individuals increased as closing time neared.

One possible explanation of these results is state-dependent valuation. For example, individuals place greater value on food items they consumed when they were hungry versus food items they consumed while they were satiated (Hemingway et al. 2020; Pompilio et al. 2006). Pennebaker et al. offered another explanation based on the psychological theory of dissonance: “If the subject were committed to going home with the person of the opposite sex, it would be dissonant to consider an unattractive partner. The most efficient way of reducing such dissonance could be to increase the perceived attractiveness of the prospective alternatives.” If so, the next morning the judging person would not experience cognitive dissonance along with his hangover.

Alcohol was one key variable that was not controlled in the closing time study. The beer goggles effect is well known and a number of studies have documented how blood alcohol content (BAC) by itself influences perceptions of attractiveness (Lyvers et al. 2011). The Pennebaker study was replicated in Australia in which closing time as well as BAC was measured (Johnco et al. 2010). Both of these factors contributed independently to the closing time effect. The closing time effect generated a number of other studies of humans, but it also inspired one of our studies of túngara frogs.

Although male túngara frogs spend many nights at the chorus advertising for females, females only attend the chorus on the night they mate. If they do not mate by the end of the night they drop their eggs without being fertilized. It takes the female another six weeks to yoke up another set of eggs, a substantial time given that the breeding season is only about six months long and males and females both seem to live less than a year. Lynch et al. (2005) conducted a repeated-measures test in which females were tested early in the evening and then late in the evening, about the time they would normally drop their eggs if not mated. The females were tested with a synthetic call that was a “hybrid” between the call of the túngara frog and another species. Females were tested in one-choice tests to determine if the signal was attractive enough to elicit female phonotaxis. Early in the evening, only 29 percent of the females were attracted to this call. Later in the evening more than half of the females, 53 percent, found this call sufficiently attractive. Not only was there a significant closing time effect on call acceptance, the latency to respond to the signal was significantly faster later in the night, 404 versus 617 seconds.

Closing time can occur in different contexts. In Pennebaker’s study and the frog study, closing time referred to the nightly end of the sexual marketplace. Another “closing time” that occurs in humans is the phase of ovulation. Haselton and her colleagues tested their “fertility ornamentation” hypothesis by examining how women dress during the fertile and nonfertile periods of their menstrual cycle (Haselton et al. 2007). Women were photographed during each stage and the photographs were shown to judges. In accord with the researchers’ predictions, women were judged as being more attractive during the ovulatory phase than the nonovulatory phase, the effect being due to the women’s dress. In another study, Haselton showed that females spoke in higher-pitched more feminine voices during the fertile period (Bryant and Haselton 2009).

A biological clock in women at a much larger scale marks the countdown toward menopause, at which time reproduction is no longer an option. Easton and her colleagues propose that women have a “reproduction expediting psychological adaptation” (Easton et al. 2010: 516). In translation, this predicts that women should be more interested in sex when they are older. The research supports this hypothesis as middle-aged women not only fantasize about sex more than younger women but actually have more sex.

Male fruit flies also exhibit greater interest in sex when they are older, and at the mechanistic level we know why. Males have mature sperm two days after they emerge from their pupal case. But these males are less fertile than males that are seven days old. For ↳ both females and males, mating shortens their life, so it was predicted that males should delay mating with females until they are older and more sexually mature. This is what the researchers found (Lone et al. 2015). What is modulating this difference in sexual motivation? Males detect female pheromones with olfactory receptor neurons. When the researchers recorded neural responses to female pheromones in these olfactory receptors they showed that the neurons were one hundred times more sensitive in seven-day-old males than in two-day-old males, explaining at a mechanistic level why males were more ready to mate at an older age.

Perceptual Fluency

The field of neuroaesthetics strives to understand the cognitive and neural mechanisms underlying our appreciation for things beautiful. An intriguing idea, which has had its influence on at least one study of animal mate choice, is that of perceptual fluency. This idea was suggested by Reber et al. (2004, 364), who stated that “the more fluently perceivers can process an object, the more positive their aesthetic response.” One type of fluency includes sparse coding. This is when an object is encoded in the brain by the firing of relatively few neurons, such as a feature detectors or grandmother cells. This is in contrast to dense coding when a large number of neurons are used to encode a stimulus.

Some support for this study was suggested by Renoult et al. (2016) who trained neural networks modeled after the human primary visual cortex to recognize natural scenes. These models were then presented with women’s faces and the amount of neural activity was estimated. Men were then shown the same photographs of women’s faces and asked to score attractiveness. The degree of sparse coding explained a significant amount, 17 percent, of the variation in ratings of the women’s facial attractiveness. Our visual cortex is important in appreciating visual beauty, but it surely did not evolve to encode facial attractiveness.

The researchers suggest that the details of visual encoding probably evolved under selection to extract information about the visual world around us. This somewhat parallels finding by Changizi et al. (2006) who proposed a similar hypothesis to explain the evolution of forms used in written alphabets. There was a strong correlation between the forms of letters and the patterns in natural visual scenes.

How might this apply to animal mate choice? Renoult, Mendelson, and others (Renoult and Mendelson 2019) suggested that the hedonic value of perceptual fluency might underlie the motivation of females to seek out males with certain visual courtship patterns. This was tested by Mendelson and her colleagues (Hulse et al. 2020) with darters. These freshwater fish have a variety of habitats, and males exhibit conspicuous patterning during the breeding season. The researchers characterized the spatial statistics of the habitat and male and female color patterns using spatial Fourier analysis. For each measure, they plotted power over frequency and used the slope of that relationship to describe the pattern. The researchers showed that the pattern of the males' courtship coloration significantly ↳ matched the local habitats; females showed no such congruence with habitat, and thus it seems unlikely that camouflage is what drove this pattern in the males.

These studies of perceptual fluency are important contributions to sexual selection. If females gain hedonic value from interacting with certain traits this goes a long way in supporting Darwin's notion of sexual aesthetics.

Summary

Cognitive psychology and cognitive neuroscience have made great strides in understanding how human and human-model systems analyze information to make informed decisions. These fields have already had an important influence on animal foraging behavior (Kacelnik 2006), but less so on animal mate choice.

With the resurrection of interest in sexual selection in the 1970–1980s, studies of animal mate choice mostly focused on signal content of male courtship displays and the adaptive significance of female mate choice. Eventually, interest turned toward integrating evolutionary and mechanistic studies to get a deeper understanding of animal sexual aesthetics. Most recently, a number of researchers have been addressing issues related to the role of cognition in mate choice, and as I have shown here, many of these studies are inspired by research typically conducted in humans. I suggest that studies in cognitive psychology and cognitive neuroscience contain a trove of potential insights into how animals make mate choice decisions. Such integration and interaction will not only give insights about mate choice but allow us, at a more global scale, to evaluate the degree of continuity or noncontinuity between the mind of the animal and the mind of the human (Cheney and Seyfarth 2008; Griffin 2013).

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