BACK TO THE BASICS OF MATE CHOICE: THE EVOLUTIONARY IMPORTANCE OF DARWIN'S SENSE OF BEAUTY

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ABSTRACT

There is a simple and general explanation for the evolution of mate choice that does not rely on benefits to be gained from favoring some potential mates over others, nor on ornament-preference genetic correlations (but that can help establish such benefits and correlations). Mate choice necessarily arises from competition to engage the powerful but discriminating reward mechanisms that regulate sexual interactions. Progress in understanding the evolution of mate choice will come from analyzing the subjective nature of the cognitive-emotional mechanisms that regulate its expression. A key mechanism may be the sense of beauty — the feeling whose function it is to reward attention to, and engagement with, attractive objects. Any animal whose behavior and decision making are regulated by mechanisms of emotion and feeling may possess the sense of beauty. Competition to be perceived as beautiful engages brain-generated, top-down influences on perception and subjective experience, adding manifold ways to improve ornament attractiveness. I discuss the evolutionary consequences of mate choice involving the sense of beauty, and how to test for it.

KEY WORDS

cognitive phenotype, runaway, sense for the beautiful

INTRODUCTION

As a natural phenomenon, mate choice has the distinction of being the solution to a big problem, yet being itself a problem in need of a solution. Mate choice explains why extravagant sexual ornaments evolve. But mate choice itself is extravagant and needs explanation. In outlining mate choice as one of the two causes of sexual selection, Darwin (1871) amassed evidence that mate choice is widespread in nature, and discussed some cognitive-emotional mechanisms involved in its expression. But he did not explain why it evolves — or did not seem to, which is perhaps one reason why his proposals of natural selection and of sexual selection due to male-male antagonism were accepted much earlier than his proposal of sexual selection due to mate choice. But ever since mate choice was understood to be widespread in nature, the need to explain its occurrence has been a main motivation of research on evolution and behavior (Andersson 1994; Andersson and Simmons 2006; Rosenthal 2017).

Seeking to explain the evolution of mate choice, biologists have discovered many possible reasons why animals might favor some potential mates over others, rather than mate randomly or with the first option encountered. These possibilities constitute a byzantine edifice of benefis and costs of male-female interactions; trait developmental and genetic architectures; co-option of perceptual mechanisms; and modes of male-female coevolution — it is difficult to gather all this under a single conceptual framework (Cronin 1991; Andersson 1994; Kokko et al. 2006; Kuijper et al. 2012; Rosenthal 2017; Alonzo and Servedio 2019). There is theoretical and empirical support at varying levels for all of these proposals, but decades of research and debate have not advanced the field towards a consensus explanation (Kuijper et al. 2012; Prum 2017; Rosenthal 2017; Ryan 2018; Patricelli et al. 2019; Achorn and Rosenthal 2020).

But what if Darwin's framework encapsulated the necessary components to explain the evolution of mate choice? For this to be the case, the framework would have to reconcile and unify the variety of avenues of thought that have addressed mate choice — benefits and costs, male-female conflict, whether and how ornaments and preferences coevolve, and the role of aesthetic evaluation in it all. Darwin's framework would have to provide:

(i) a reason why mate choice evolves that does not rely on (but sets up) benefits of choosing;

(ii) a reason why sexual ornaments and mate preferences coevolve that does not rely on (but sets up) ornament-preference correlations; and

(iii) a reason why the cognitive-emotional mechanisms of mate choice, including the potential for aesthetic evaluation by animals, influence the evolutionary dynamics that they generate.

Here I argue that Darwin's framework, with its mechanistic focus, does provide the above elements, when integrated with current knowledge of male-female evolutionarily stable strategies; the causes of variation in ornaments and preferences; and the cognitive-emotional nature of the regulation of behavior in animals.

MATE CHOICE EVOLVES EVEN WITHOUT BENEFITS OF CHOOSING

To understand any adaptation, the benefits it may bring are the wrong starting point. Benefits may be incidental, and can mislead analyses of how adaptations evolve (Williams 1966; West-Eberhard 1992). (Further, the nature of sexual selection makes it likely that incidental benefits of mate choice will arise; see below.) To understand adaptations it is necessary to analyze whether and how they have been designed (modified by selection) to perform specific functions (Williams 1966; West-Eberhard 1992).

In terms of functional design, the most basic fact about the mechanisms that regulate sexual engagement is that they must be sexually dimorphic. This is because of the sex difference in the relationship between reproductive success and mating success — with males predominantly having a steeper (or less plateauing) reproductive success~mating success function than females. This sex difference is widespread in animals and plants and ultimately arises from anisogamy (Trivers 1972; Kokko et al. 2006; Janicke et al. 2016; Tonnabel et al. 2019).

From this sex difference, there follows a corresponding dimorphism in the mechanisms that regulate sexual engagement (Figure 1A): These mechanisms must provide strong motivation to mate (according to the absolute fitness consequences of failing to do so). However, while both sexes must be strongly motivated to mate, the sex with the shallower or plateauing function (predominantly females) is strongly motivated to mate *but with only a subset of potential mates*, beyond which they do not benefit from additional matings. The mechanisms must be powerful in both sexes, but necessarily more discriminating in one sex.

Sexual dimorphism in the mechanisms that generate and sustain sexual engagement has a further consequence: There must necessarily be competition within one sex (predominantly males) to engage the reward mechanisms of the more selective sex (predominantly females) (Figure 1B). Variation in the ability to engage these mechanisms (e.g., variation in males' ability to induce females to tolerate being approached) necessarily results in mate choice (Figure 1C).

A further key feature in these reproductive dynamics is that the discriminating sex is selected to remain discriminating *regardless of the overall attractiveness of the suitors*, in order to keep its number of matings near optimum. Mate choice is therefore sustained indefinitely, as long as (and, crucially, as soon as) there is variation in the competing sex in the ability to engage the reward mechanisms of the selective sex (Figure 1C).

Thus, the origin and maintenance of mate choice are adaptive, involving adaptations that regulate sexual interactions and optimize the number of matings for each sex. However, the origin and maintenance of mate choice do not require benefits from favoring some potential mates over others *per se*. This argument is implicit in the expositions by Darwin (1871) and West-Eberhard (1983, 2014). Here I simply make it explicit, and back it with the now well-established sex difference in reproductive success~mating success functions (Janicke et al. 2016; Tonnabel et al. 2019). Note that the argument is a "light" version of the hypothesis of sexually antagonistic coevolution (Holland and Rice 1998; Arnqvist and Rowe 2005) — except that it emphasizes selective cooperation with preferred males rather than general antagonism (Cordero and Eberhard 2003). This rationale also applies under sex-role reversal and mutual mate choice (Rodríguez 2015), as long as there is a sex difference in the function relating reproductive success to mating success.

Against the above rationale for the origin and maintenance of mate choice, it might be argued that the female mechanism for regulating the number of matings could simply consist of high motivation to mate with the first option encountered (or with the first *n* options), then shutting down all sexual engagement. A mechanism like that would regulate the number of matings but result in no mate choice. Such scenarios can occur when females rarely or never encounter more than one male at a time; e.g., in range-guarding mating systems, where males defend a territory that overlaps with those of one or several females, as in some mammals (Clutton-Brock 2016); in species where females mate with a brother immediately upon maturation, as in some parasitoid wasps (Thornhill and Alcock 1983); or in low-density or endangered species. But those are cases in which there is no mate choice — the regulation of sexual engagement by females is a function of the mating system, not of female mating decisions. Very often, however, at least a few males are present (Thornhill and Alcock 1983; Andersson 1994; Roff and Fairbairn 2014; Clutton-Brock 2016). Thus, when the regulation of sexual engagement in females involves mating decisions, it predominantly requires selectivity among several options. Under such conditions, any rule females might use to mate with the first option (e.g., mate with nearest suitor) would nevertheless generate competition among males and mate choice (e.g., competition to be perceived as the nearest, selecting for higher-amplitude courtship signals or larger ornament or body sizes).

MATE CHOICE SETS UP THE BASIS FOR BENEFITS OF CHOOSING

Sexual selection is stronger and steadier than natural selection (West-Eberhard 1983, 2014; Hoekstra et al. 2001; Kingsolver et al. 2001; Hereford et al. 2004; Svensson et al. 2006; Siepielski et al. 2011). Consequently, ornaments and displays often become elaborate in costly ways, coming to reflect more and more aspects of the bearer's genotype and condition. This is the crucial insight of the genic capture model (Rowe and Houle 1996), and is expected under a broad range of mate choice scenarios (Lorch et al. 2003; Chandler et al. 2013). Correlations between ornament features and the bearer's condition or viability can therefore arise *even if there is no selection for mate choice to favor individuals with high viability or condition* — they arise incidentally from the nature of sexual competition under mate choice (Figure 1D). Even absent such correlations, favoring more elaborate or simply more detectable displays may have incidental beneficial consequences, such as shortening mate searching times (Ryan and Cummings 2013).

Once present, ornament-quality relationships may contribute to subsequent selection on mate choice (Figure 1E), as they may now influence the number, viability, or attractiveness of females' offspring (i.e., as per the traditional view of mate choice benefits; Andersson 1994). Further, females are selected to minimize the cost of sexual interactions and to favor males that afford them greater freedom of action and choice (West-Eberhard 2014; Prum 2017; Snow et al. 2019), sometimes even evolving to provide feedback on how to be courted (Patricelli et al. 2002; Peretti et al. 2006; Rodríguez 2015), thereby increasing the likely import of benefits relative to costs.

The key point in this argument, however, is that the origin and maintenance of mate choice do not require ornament-quality or ornament-benefit relationships, or benefits of mate choice *per se* (Figure 1C). From this vantage point, the state of the art in the “good genes” literature — ornament-quality relationships that involve multifarious traits and dimensions of quality across species, and that are weak on average (Møller and Alatalo 1999; Prokop et al. 2012; Rosenthal 2017; Achorn and Rosenthal 2020) — looks like support for the hypothesis that mate choice benefits arise incidentally from the process of ornament elaboration, with potential subsequent consequences for selection on mate choice. If ornaments are not selected as quality indicators, but evolve some relationship with quality due the dynamics of sexual selection, they would not necessarily be especially good indicators of quality. (From another perspective, the “good genes” literature provides a trove of information on the genetic, developmental, physiological, and metabolic architecture of sexual ornaments and displays — on the variety of forms by which ornaments and diplays are constructed.)

Doubtless there are cases where mate choice is in fact selected to obtain benefits that increase the chooser's fecundity (e.g., choice favoring high quality nests or nuptial gifts) (Andersson 1994; Wagner 2011). In such cases, mate choice does indeed evolve to attend to benefit indicators (e.g., nest features). But in such cases mate choice is explained by natural selection, as it hinges on female fecundity (West-Eberhard 1983, 2014), and is not extravagant or puzzling. For example, a species where females choose purely on the basis of the quality of the nest built by males and no other feature or decoration of the nest or of the male would not present a problem in need of a special explanation. By contrast, the above argument (that the evolution of mate choice does not require, but sets up, benefits of choice) addresses the large proportion of cases where mate choice does pose such a problem because of the extravagant nature of the ornament and the mate choice behavior; e.g., at leks (Andersson 1994; Höglund and Alatalo 1995).

MATE CHOICE SETS UP THE BASIS FOR ORNAMENT-PREFERENCE RUNAWAYS

As discussed above, females are continually selected to accept only a subset of mates (beyond which they no longer benefit from additional matings). Therefore, as males in the population improve in their ability to be accepted, females are selected to become more discriminating, simply to retain their ability to accept only the number of mates or matings from which they benefit. This, by itself, generates ornament-preference coevolution, regardless of whether any other evolutionary mechanisms (such as Fisherian runaways involving linkage disequilibrim; see below) are at play (Figure 1C). Further, when males evolve different ways to improve their attractiveness, females are selected to become more discriminating *of those features that have* *evolved to improve ornament attractiveness.* This, by itself, generates ornament-preference co-divergence. This too is a "light" version of the chase-away model under sexual conflict (Holland and Rice 1998), except that, as noted above, it emphasizes selective cooperation rather than antagonism with all males (Cordero and Eberhard 2003).

Thus, ornament-preference coevolution can occur regardless of whether ornament-preference genetic correlations exist. Nevertheless, the assortative mating resulting from the basic operation of mate choice sets the foundation for such correlations to arise, given genetic variation in the ornament and the preference (Fisher 1958; Mead and Arnold 2004; Henshaw and Jones 2020) (Figure 1D).

THE NATURE OF THE COGNITIVE-EMOTIONAL MECHANISMS OF MATE CHOICE

Darwin (1871) cast his explanation of mate choice in terms of a "sense of beauty". He used this term in two ways: In some passages he simply meant that animals may be more attracted by some potential mates than others. For example, he asks the reader:

"*Does the male parade his charms with so much pomp and rivalry for no purpose? Are we not justified in believing that the female exerts a choice, and that she receives the addresses of the male who pleases her most? It is not probable that she consciously deliberates; but she is most excited or attracted by the most beautiful, or melodious, or gallant males*." (p 123)

This meaning is present throughout the book. In a later section, he reasons:

"*If it be admitted that the females prefer, or are unconsciously excited by the more beautiful males, then the males would slowly but surely be rendered more and more attractive through sexual selection*." (p 234)

In other passages, Darwin posits emotional and cognitive evaluation of potential mates. He relates the emotions experienced by humans to those experienced by animals when evaluating potential mates, and the neural and cognitive mechanisms involved in those experiences:

"*These powerful and mingled feelings may well give rise to the sense of sublimity. We can concentrate* […] *greater intensity of feeling in a single musical note than in pages of writing. Nearly the same emotions, but much weaker and less complex, are probably felt by birds when the male pours forth his full volume of song, in rivalry with other males, for the sake of captivating the female*." (p 335-336)

This meaning is also present throughout the book. Towards the end, Darwin argues:

"*Everyone who admits the principle of evolution, and yet feels great difficulty in admitting that female mammals, birds, reptiles, and fish, could have acquired the high standard of taste which is implied by the beauty of the males, and which generally coincides with our own standard, should reflect that in each member of the vertebrate series the nerve-cells of the brain are the direct offshoots of those possessed by the common progenitor of the whole group. It thus becomes intelligible that the brain and mental faculties should be capable under similar conditions of nearly the same course of development, and consequently performing nearly the same functions*." (p 401)

Thus, Darwin's framing of mate choice included a range of possibilities for the cognitive mechanisms involved. At one end, there is "unconscious excitation". Here, mate choice may be regulated by simple mechanisms. There is evidence of such cases; e.g., as few as five neurons suffice to make a band-pass filter for signal pulse pattern (Schöneich et al. 2015), and the firing behavior of single neurons may match an animal's preference behavior (Kostarakos and Hedwig 2012).

At the other end, however, there is subjective aesthetic evaluation. This is perhaps another reason why Darwin's proposal of mate choice as a cause of selection was harder to contemplate than his proposal of male-male antagonism — it seemed too much to ask of animals. Nevertheless, there is now evidence of sophisticated neuro-cognitive mechanisms involved in mate choice (Gerhardt and Huber 2002; Greenfield 2002; Ryan and Cummings 2013; Jordan and Ryan 2015; Rosenthal 2017; Ryan 2018; Ryan et al. 2019; Lynch and Ryan 2020). Recent treatments directly address hedonic (Rosenthal 2017, 2018) and aesthetic evaluation (Prum 2012, 2017). However, the subjectively-experienced nature of evaluation (the subjective nature of hedonic experience) has important evolutionary consequences that remain to be analyzed. It is not simply the case that “beauty happens” (Prum 2017). The expression of the sense of beauty in animal brains must be tested for and analyzed in order to understand its evolutionary consequences. This endeavour is now possible because advances in neuro-aesthetics offer an objective definition of the sense of beauty. And advances in the study of mental processes as cognitive phenotypes (Mendelson et al. 2016; Kilmer et al. 2017) offer objective approaches for the study of subjective phenomena such as the cognitive processes expressed in animal brains and minds.

THE SENSE OF BEAUTY

The sense of beauty is a feeling (Dutton 2009; Starr 2015). Feelings are the subjective experience of emotions, and help regulate behavior and decision-making through the subjective experiences that they generate for animals — hunger, thirst, pain, disgust, and so on (Darwin 1872; Panksepp 1998, 2011; Miller 2000; Denton 2006; Barrett et al. 2007; Mendl et al. 2010; Damasio and Carvalho 2013; Feinberg and Mallatt 2016). In other words, feelings are adaptations that function by being experienced subjectively — by being felt.

The sense of beauty is the feeling that functions to reward *attention to, and engagement with,* attractive objects (Thornhill 1998; Dutton 2009; Chatterjee 2014; Starr 2015). The attractive-beautiful distinction corresponds to Darwin's distiction between mate choice with mechanisms involving "unconscious excitation" and "emotions felt".

To posit a sense of beauty in animals is not to suggest that they have equivalent aesthetic experiences to humans — instead, it is to suggest that animals have subjective experiences as they evaluate potential mates. It is also not to say that we can fully know what those experiences are like, but that we can know something about them as parts of the decision-making process, and that we can assess their consequences. Any animal whose behavior and decision-making are regulated by mechanisms involving subjectively experienced feelings may in principle possess the sense of beauty — it may subjectively experience rewarding, attention-holding feelings as it regards attractive objects. The taxonomic range of such animals may be quite broad (Panksepp 1998, 2011; Miller 2000; Denton 2006; Damasio and Carvalho 2013; Feinberg and Mallatt 2016), including perhaps some invertebrates (Barron et al. 2010; Perry and Baciadonna 2017).

The sense of beauty may reward attention to many different kinds of objects. Many things besides potential mates can be perceived as beautiful — anything from landscapes to mathematical proofs (Dutton 2009; Lockhart 2009; Chatterjee 2014). There are, however, two important ways in which the sense of beauty has unique consequences in mate choice:

(i) In mate choice, the objects of regard compete with each other, and evolve, to be perceived as beautiful. This is not at all the case in most other contexts, where the objects of regard either do not evolve, or evolve in antagonism to their evaluation. Animals may evolve to find a cool draught of water and a plump prey beautiful, but the water and the prey are not selected to appear beautiful to the animal — quite the contrary in the case of prey, which are selected to avoid detection or to appear dangerous or distasteful. Note, however, that some objects of regard likely do evolve to be perceived as beautiful in contexts other than sexual competition; e.g., in social competition (such as with siblings competing to be perceived as beautiful by their parents), with comparable evolutionary consequences (West-Eberhard 1983, 2014; Lyon and Montgomerie 2012). Here I focus on sexual competition.

(ii) As in humans, what many animals perceive is a "virtual reality interface", a brain-generated model of their surroundings and their body in relation to their surroundings, with considerable "top-down" input from the brain (Hawkins and Blakeslee 2004; Webb and Graziano 2015; Barron and Klein 2016; Feinberg and Mallatt 2016). Such brain-generated constructs are not fully up-to-date and accurate representations of reality. Instead, much of the content of mental models at any one time is "filled in" from memory and processing heuristics — recall for example the familiar class demonstration of the optic blind spot and how most of the time we do not perceive it (e.g., Harris 2014 p 136). The range of animals that are likely to navigate the world with such mental models is a matter of current debate. But there is evidence that this is likely to be widespread at least among vertebrates, and perhaps other groups as well (Darwin 1871, 1872; Baars 1997; Hawkins and Blakeslee 2004; Barron and Klein 2016; Feinberg and Mallatt 2016).

WHY THE SENSE OF BEAUTY MATTERS FOR THE EVOLUTIONARY CONSEQUENCES OF MATE CHOICE

The features that distinguish sexual selection from natural selection, making it more dynamic and on-going, have long been recognized (Table 1A) (Darwin 1871; West-Eberhard 1983, 2014;

Prum 2012, 2013, 2017; Ryan 2018). The question is the degree to which the points discussed above (competition to be perceived as beautiful involving perception of brain-generated mental models) contribute to the distinctive features of sexual selection when mate choice is its cause (Table 1B). Suggestions that the contribution of the sense of beauty is important arise from insights noting that:

"*Being attractive to a population of conspecific 'minds' is a much less constrained problem, with a broader, potentially infinite set of possible, frequency-dependent solutions.*" (Prum 2012 p 2259)

Similarly, in the case of humans, it has been noted that evaluation aesthetic refers:

"*not primarily to something inherent in objects but to a feature of our experience of objects, perceptions, and ideas*." (Starr 2015 p 14)

These insights are correct because of the consequences of the subjective, inner-experience nature of the emotional-cognitive mechanisms that regulate mate choice. Competition to be perceived as beautiful engages brain-generated, top-down influences on perception and subjective experience. Consequently, ornaments are not mainly selected according to physical or ecological conditions — although these certainly influence and channel how ornaments evolve (Endler 1992; Maan and Seehausen 2011; Safran et al. 2013). Instead, ornaments evolve under selection stemming primarily from an emotional-perceptual-cognitive landscape consisting of the perceptions and evaluations of the individuals that observe them. This constitutes a fitness landscape that offers many more opportunities to enhance attraction than would one primarily determined by the ecological environment or by "unconscious" (i.e., non-subjectively experienced) mechanisms.

But why would the problem of being attractive to conspecific minds be "much less constrained" than a problem not involving those minds? (Prum 2012). There are several features of the sense of beauty that increase the variety of ways in which suitors can evolve to solve the problem of competing to be perceived as beautiful, as follows:.

The sense of beauty may compensate for deficient ornament features

As noted above, what many animals perceive is a brain-generated model with much of the detail filled-in from memory and processing heuristics. Consider, for instance, the phenomenon of perceptual rescue, whereby incompletely presented objects are perceived as whole. Thus, a dog seen through a picket fence is seen as a whole animal, not a series of slices; similarly, a sound with all of the components of an overtone series except the fundamental frequency is nevertheless perceived as having the fundamental (Levitin 2007; Klump 2016). Perceptual rescue is multimodal. For example, Túngara frog males produce a "whine-chuck" mating call that loses attractiveness to females when the whine and chuck elements are separated by a silent interval; however, attractiveness can be recovered by inserting a visual stimulus of a calling male into the silent interval: females perceive that out-of-phase acoustic-visual sequence as an attractive whole Taylor and Ryan 2013). An extreme example of multimodal filling-in: humans tend to deem beautiful people as more likely to show goodness, competence, innocence, etc. (Chatterjee 2014) — on the basis of one virtue, we fill-in additional virtues.

Due to perceptual phenomena like filling-in and perceptual rescue, once an individual’s ornament activates the sense of beauty in an observer, it may be “forgiven” some less than perfectly attractive features — the observer may fill them in. Further, the related notion from Gestalt theory that perception in ambiguous circumstances converges on the most regular and symmetric percepts that are consistent with the available sensory inputs (Rock and Palmer 1990) means that processing heuristics may, by themselves, tend to improve the beauty of the objects perceived. Such phenomena are likely to be common: there is strong evidence that perception in a wide variety of animals follows Gestalt principles (Dent and Bee 2018).

The sense of beauty draws from memory and anticipated rewards

In humans, aesthetic experience involves imagination, memory, and anticipation (Thornhill 1998; Chatterjee 2014; Starr 2015). An object perceived as beautiful evokes not only a desire to continue to observe it, but also to engage with it, and to anticipate what it would be like to engage with it. This is probably the case at least to some extent in many animals.

There is abundant evidence of learning and experience-mediated plasticity as causes of variation in courtship behavior and mate preferences and mate choice decisions (Guilford and Dawkins 1991; Hebets and Sullivan-Beckers 2010; Verzijden et al. 2012; Rodríguez et al. 2013b). It therefore seems likely that prior experience may influence the mechanisms of subjective experience involved in mate choice. Prior rewarding encounters with some mate types may tinge memory with positive feelings (with the anticipation of another rewarding experience), so that what was once merely attractive may subsequently become beautiful, or more beautiful. Conversely, negative encounters may tinge with ugliness something that was initially attractive. Because individuals will vary in which encounters with which mate types were positive or negative, individual life trajectory may influence subsequent perceptions and evaluations.

Note that learning and experience are not only likely to influence the evaluation of courtship but also its production (except for ornaments that are purely outgrowths of the body and require no behavior to be exhibitted). Thus, the potential for novel variants in ornaments and displays may often be as great as the potential for novel evaluations (Table 1).

With the sense of beauty, competition for attention is inherently multivariate and multimodal

To compete to be perceived as beautiful is to compete to attract and hold the subjective attention of observers. Novel ways of drawing and holding attention may be effective without change in the "main" features of the ornament. Imagine a species in which the males have a red ornament that they display over their head, and the females prefer brighter ornaments. To make himself more attractive in terms of an "unconscious" (in Darwin's sense) mate preference, a male would have to increase the brightness of his ornament. But a male could make himself more beautiful without changing his brightness by, say, slightly waving his ornament (or by growing a curl at the top the ornament or a constrasting spot in the middle). A miriad little changes in how an ornament is displayed or moved may thus engage the sense of beauty. Such changes might increase attractiveness by simply improving detectability or reducing habituation, with no involvement of a sense of beauty. However, the sense of beauty in a brain attentive in different modalities and with systems rewarding subjective attention would be more likely to respond to a wider variety of changes.

If adding a quirk of movement, shape, or color to an ornament improves its attention-getting power, and hence its beauty, ornaments that start out simple may quickly evolve to be more complex, with additional modalities of signaling being recruited to be part of the ornament. Thus, the sense of beauty allows for ways to improve on beauty that do not require change in the underlying "unconscious" preference that defines "baseline" attractiveness.

The sense of beauty facilitates recruitment of perceptual biases into mate choice

One of the more remarkable discoveries to arise from research on animal communication is the widespread evolution of novel ornament features that co-opt receiver responses and sensibilities that originally evolved in non-sexual contexts (West-Eberhard 1984; Christy 1995; Ryan 1998; Rodríguez and Snedden 2004; Ryan and Cummings 2013; Ryan 2018). This co-option has contributed to the great diversity of sexual ornaments seen in nature by recruiting species differences in ecology and sensory processing into the dynamics of sexual selection (West-Eberhard 1984; Rodríguez 2009; Ryan 2018). Ornament features that co-opt perceptual biases range from food-mimicking to predator-mimicking devices, and include most if not all sensory modalities. Extreme cases involve lineages that do not naturally express mate choice at all, where novel ornaments can induce mate choice *de novo* (Gould et al. 1999).

How is it possible that novel ornament features so often co-opt receiver responses that evolved (and, until co-option, were only ever expressed) in non-sexual contexts? The answer may often involve the sense of beauty. Animals that navigate the world through a multi-modal model of their surroundings, filling-in details from top-down inputs influenced by memory and anticipation may be more likely to incorporate non-sexual aspects of their model into their evaluation of sexual ornaments than animals lacking such processing. This may help explain how novel ornament features cross contexts, from the ecological to the sexual.

Limits

There are two main sources of limits to the contributions of the sense of beauty to sexual selection. First, there is the long-recognized risk of performing excessively showy displays or spending too much time in evaluation (Andersson 1994). Second, there are limits that arise from how brains process complex signals. There may be displays that are too elaborate or too chaotic for an observer's processing capabilities. Beauty may therefore entail a balance between monotony and complexity (Hartshorne 1992). Indeed, there is evidence from the field of neuroaesthetics that the attractiveness of a stimulus is in part a function of how easily or efficiently it can be processed — of the stimulus being "easy on the eyes" (Reber et al. 2004; Chenier and Winkielman 2009; Renoult and Mendelson 2019). Stimuli that are familiar, prototypical (i.e., representative of a category), or that correspond to features that processing systems are adapted to process (e.g., natural terrestrial scenes) have greater ease of processing and are, by virtue of such ease, "pleasant" or rewarding to process (Reber et al. 2004; Chenier and Winkielman 2009; Renoult and Mendelson 2019).

Consequently, competition to be perceived as more beautiful is not merely a function of adding more and more attention-getting twists and curls. Instead, incorporating new elements may require coordination with the existing features of a display (Hartshorne 1992).

TESTING FOR A SENSE OF BEAUTY IN ANIMALS

Each of the consequences listed above may be turned into a prediction of the hypothesis; e.g., it should be possible to improve beauty with modifications external to the ornament; filling-in should rescue the beauty of ornaments categorized as beautiful; and so on. However, the main point of the sense of beauty hypothesis hinges on the evolutionary consequences of the subjectively-experienced nature of the cognitive-emotional mechanisms involved. Consequently, testing the hypothesis requires an emphasis on testing for subjective experience as a part of the mechanisms of mate choice in animals; as well as an emphasis on testing for the proposed evolutionary consequences.

Predictions regarding the involvement of subjectively-experienced mechanisms in mate choice

Evaluating potential mates (especially attractive ones) should be enjoyable

If evaluation of ornaments is subjectively rewarding, there should be evidence that animals enjoy it. It might seem trivial to say that reward mechanisms should be involved in the regulation of behavior — how could reward mechanisms *not* be involved in the regulation of animal behavior? But the point is to test for subjective experience of those rewards, because of the important consequences that follow from it.

There are various ways to test this prediction. One is through study of hormonal/neural anticipatory/reward networks. For example, dopamine levels should increase in anticipation of, and during, evaluation of courtship. There is evidence suggestive of a role for dopamine in signal evaluation by female frogs (Endepols et al. 2004; Hoke et al. 2007; Lynch and Ryan 2020), as well as in the regulation of sexual receptivity in female fruit flies (Neckameyer 1998; Ishimoto and Kamikouchi 2020). (Further, dopamine and related hormones have been shown to help regulate foraging decisions in insects; Perry et al. 2016; Peng et al. 2020).

Another way to test this prediction: if evaluation of potential mates is enjoyable, it should reach excessive or extravagant levels. By excessive I mean well beyond the requirements of sampling, making distinctions between individuals, and receiving any amount of stimulation necessary to trigger physiological processes such as ovulation — evaluation performed purely because it is enjoyable.

"Excessive" evaluation may seem too fuzzy a criterion to be useful. However, tests could first determine the amount of assessment that animals require in order to make mate choice decisions, and then compare that to the amount of assessment that the animals actually perform. For example, acoustic playback experiments with frogs have provided a wealth of information on mate choice decisions and mate preferences (Gerhardt and Huber 2002; Ryan 2018). Such experiments typically present females with one, two, or several stimuli, and determine which stimulus is approached by the females, and how quick the approach is. In such trials, females typically very quickly localize, decide between options, and approach a stimulus — in a few seconds or minutes. By contrast, studies of natural pair formation in the field show a different picture. For example, wrinkled toadlet females dedicate several nights to moving among signaling males, listening for up to three hours to each one, before finally approaching one to solicit a mating (Robertson 1986). Barking treefrog females make their decision in a single night, but their approach to a male chorus takes several minutes along which they repeatedly pause, moving quickly only in the final approach to their chosen male (Murphy and Gerhardt 2002). Similar pause-and-listen intervals have been documented for other frogs as well (Ryan 1985 p 41-44; Arak 1988; Schwartz et al. 2004). Finding and assessing potential mates is doubtless more challenging in nature than in a bioacoustics lab (e.g., Lee et al. 2017). "Real world" difficulties could explain slower approach times in nature, but I suggest that they do not explain behaviors such as "deliberate" repeated pauses dedicated to listening, nor multiple rounds over several days. If it could be ruled out, for instance, that wrinkled toadlet females require several nights of stimulation by a chorus to initiate/complete egg development, then those repeated rounds of evaluation might begin to fit the criterion of “excessive”. Or if it could be ruled out that barking treefrogs do not simply pause during intervals of, say, higher noise in the chorus — and there is evidence that noise oscillations do not affect phonotaxis in another treefrog (Vélez et al. 2012) — then those pauses might also begin to fit the criterion of “excessive". In extreme cases, females delay the process having already made a choice: female túngara frogs bump calling males they have already approached to elicit more of their preferred “chuck” call element (Akre and Ryan 2011; Ryan 2018).

Another potential example: In satin bowerbirds, females evaluate male behavioral displays and their bower decorations over three rounds, each lasting several days: in the first round females assess bower decorations absent the male, and in the second and third rounds they assess the males’ displays (Uy et al. 2001; Coleman et al. 2004). Younger females mainly attend to bower decorations, while older females mainly attend to the displays; male displays are similar to those they use in aggressive male-male encounters, and sometimes startle the females, but males modulate the intensity of their displays according to feedback from the females' posture about their perceived level of threat (Patricelli et al. 2002, 2004; Coleman et al. 2004). These rounds of evaluation and back-and-forth adjustment of display intensity seem to be well beyond any practical requirement for making distinctions or receiving stimulation. It might be argued that this process is like a job interview, where sequential assessment of various features of the candidates is required. But note the key role of female subjective reactions (e.g., whether they feel threatened or not) to male decorations and displays.

The “excessive evaluation” prediction also states that it should be the most attractive individuals that are evaluated for the longest. Specifically, this prediction does no refer to the difficulty of deciding between similar, attractive options (e.g., Bosch et al. 2000; Bosch and Márquez 2005; Höbel 2016; Hemingway et al. 2019; Stratman and Höbel 2019). Instead, clear "winners" should be inspected (should be enjoyed) the longest.

Another way to test the prediction may be to ask whether animals pay attention to ornaments or displays outside the immediate context of mate searching. Due to the naturally-selected costs of extravagant signaling and mate assessment, it seems likely that the sense of beauty should be down-regulated in the off-season. However, it may not be entirely switched off. Thus, this prediction is asymmetric: support would be informative, but lack of support could be due to down-regulation of the sense of beauty. Nevertheless, there are suggestive field observations: female lance-tailed manaquins sometimes observe male displays off the mating season (DuVal 2007).

The prediction could also be tested in learning or training experiments. If evaluating displays is rewarding, exposure to displays should serve as a reward in such experiments. In other words, exposure to displays could take the place of food rewards to train animals to perform arbitrary tasks by associating the target behavior with a reward consisting of exposure to an attractive ornament or display.

Performing courtship displays should be enjoyable

The rationale that evaluating potential mates should be enjoyable also applies to the expression of courtship behavior, such as bird song and dance. With the sense of beauty, animals should enjoy their performances (Hartshorne 1992; Miller 2000; Prum 2017). Tests of this prediction are analogous to the above. Enjoyment should be revealed, for instance, in the activation of hormonal/neural networks; in “excessive” performances, especially by the better performers; in out of season performances; and so on. There is support for a range of these predictions: Dopamine is released before and during courtship/sexual behavior in birds and rats (Hull and Dominguez 2006; O’Connell and Hofmann 2011). Singing in birds is rewarding by itself (Riters et al. 2014, 2019; Hahn et al. 2017), and is performed outside the breeding season (Riters et al. 2014, 2019). Note, however, that this prediction refers to performance of an animal’s own courtship displays. The displays of competitors, however, may be unpleasant (Earp and Maney 2012).

The expression of the sense of beauty should be regulated by the same areas of the brain regardless of the sensory modality of courtship

A top-down mechanism that rewards attention to beautiful objects requires a specific brain area or network of areas to generate the feeling or emotion of contemplating beauty. This area or set of areas should be activated whenever an animal observes an object that it finds beautiful, regardless of the sensory modality involved (of course other parts of the brain involved in perceiving the respective modalities will also be activated). Nevertheless, there should be a common “core” activated across modalities. (But see Chatterjee [2014] for a different expectation.)

This prediction can be tested in two ways. First, for any given species, perception of beautiful objects through different modalities should be seen to activate a common core of brain areas. There is evidence in support of this prediction in humans. Perception of visual, auditory, taste, and scent stimuli as beautiful all involve activation of the medial orbitofrontal cortex (Rolls et al. 2003; Kringelback 2005; Kim et al. 2007; Brown and Dissanayake 2009; Veldhuizen et al. 2009; Ishizu and Zeki 2011; Chatterjee 2012; Kirk 2012). Interestingly, the medial orbitofrontal cortex is also involved in enjoyment and anticipation of rewards (Kringelback 2005; Chatterjee 2014, p 77-78), a key aspect of the sense of beauty (see above discussion). Similarly, erotic visual stimulation induced activation in the same regions according to the sexual orientation, but not the sex, of the subject (Mitricheva et al. 2019).

Second, closely related species with ornaments in different modalities (say, sp. V has an exclusively visual display whilst sp. A has an exclusively auditory display) should conduct aesthetic evaluation with the same brain areas. There is evidence that such commonalities extend beyond closely related species. For instance, when female white-throated sparrows with breeding-typical hormone levels were presented with male song, they showed neural responses in the mesolimbic reward pathway that correspond to those of humans listening to agreeable music (Earp and Maney 2012). Indeed, the neural and gene expression networks that regulate social decision making are highly conserved across vertebrates (O'Connell and Hofmann 2012), suggesting a potentially widespread role for subjectively experienced rewards.

Prediction regarding the evolutionary consequences of the sense of beauty

Mate choice without the sense of beauty should produce less extravagance and slower evolution

Darwin (1871) contrasted sexual selection in animals with and without the cognitive powers to generate a sense of beauty:

"*In the lower divisions of the animal kingdom, sexual selection seems to have done nothing: such animals are often affixed for life to the same spot, or have the two sexes combined in the same individual, or what* *is still more important, their perceptive and intellectual faculties are not sufficiently advanced to allow of the feelings of love and jealousy, or of the exertion of choice*." (p 396)

It is now clear that Darwin underestimated how widespread the action of sexual selection would turn out to be (Eberhard 1985, 1990, 1996, 2009). And he probably also underestimated how widespread the cognitive machinery that can give rise to subjective experience and the sense of beauty may be (Panksepp 1998, 2011; Miller 2000; Hawkins and Blakeslee 2004; Denton 2006; Damasio and Carvalho 2013; Barron and Klein 2016; Feinberg and Mallatt 2016). Nevertheless, in spite of these underestimates of Darwin's, a counter to the sense of beauty hypothesis is that there seems to be no difference in the extravagance and speed of divergence between cases where the sense of beauty *might* be involved in sexual selection (e.g., bird song) and cases where it seems it *might not* be involved (e.g., insect and spider genitalia). Indeed, the role of cryptic mate choice in generating the astonishing patterns of divergence and extravagance in genitalia is one of the most remarkable recent advances in the study of evolution and sexual selection (Eberhard 1985, 1990, 1996, 2009; Arnqvist 1998; Peretti and Aisenberg 2015; Eberhard and Lehmann 2019).

But Darwin's prediction might nevertheless be applicable with careful distinctions between cases where the sense of beauty may or may not be involved. To the extent that animals' mental models of their bodies in relation to their environments include their genitalia, and to the extent that sensory structures in animal genitalia generate rewarding feelings (e.g., as in humans; Fleischman 2016), animal genitalia may evolve to engage the reward mechanisms of sexual engagement; e.g., male genitalia may evolve shapes, textures and movements that increase pleasure in females, and female genitalia may evolve to become increasingly discriminating in the rewarding feelings they generate. If so, the sense of beauty may be involved in the evolution of at least some dramatic cases of high elaboration and rapid divergence in genitalia.

The best current chance for comparisons between sense of beauty vs. no-sense of beauty cases may involve contrasts not between different animal species, but between different mechanisms that function at organismal versus suborganismal levels — the latter with no possibility of brains and subjective experience. Useful case studies could deal with sperm-egg or pollen-stigma/ovum interactions in animals and plants, respectively, or gamete-gamete and gamete-hyphae interactions in fungi. These cases should still bear the hallmarks of sexual selection (species-specificity and rapid divergence) (Eberhard 1996; Skogsmyr and Lankinen 2002; Nieuwenhuis and Aanen 2012), but nevertheless lack the effects arising from the sense of beauty. Consequently, they should exhibit *relatively lower* levels of extravagance and elaboration.

Making such comparisons will be challenging, to say the least. One important requirement will be a metric that can compare amounts of divergence and elaboration across very disparate kinds of traits. For this purpose, standardizing species differences by dividing by the standard deviation will occlude the predicted differences in amounts of divergence. Consequently, standardizing by the grand mean for each group or clade may be more indicated (e.g., Arnqvist 1998; Rodríguez et al. 2013a). (See also Safran et al. 2012 for an alternative approach.)

Note that sexual selection without the sense of beauty could *still* be capable of producing more extravagance and rapid divergence than natural selection (Table 1A) (West-Eberhard 1983, 2014. The question is whether and what the sense of beauty adds to the recognized powers of sexual selection (Table 1B).

DISCUSSION

A Darwinian analysis of the cognitive-emotional mechanisms of mate choice offers a broad framework that can unify the variety of avenues of research that biologists have pursued to explain the evolution of mate choice. This analysis offers a reason why mate choice is a default condition of sexual reproduction that does not need benefits of mate choice to be present, but sets up the conditions for such benefits to arise (Figure 1). It also offers a reason why ornament-preference co-divergence does not require any particular form of ornament-preference correlation, but sets up the conditions for such correlations to arise (Figure 1). Finally, it suggests that the nature of the cognitive-emotional mechanisms of mate choice influences in important ways the evolutionary consequences of mate choice (Table 1), putting a premium on testing for a sense of beauty in animals.

Runaways and the sense of beauty

The most direct treatment of the sense of beauty to date prioritized Fisherian runaway selection as the mechanism of ornament-preference coevolution (Prum 2010, 2017). This seems to weaken the hypothesis (Borgia and Ball 2018; Futuyma 2018), because ornament-preference genetic correlations have overall been found to be weak (Greenfield et al. 2014).

There are several important points to make regarding runaways. First, as discussed above, ornament-preference coevolution arises from selection on females to remain both motivated to mate and discriminating, while males are selected to improve in their ability to be accepted. This results in ornament-preference coevolution regardless of whether genetic correlations are present (as long as ornaments and traits have the capacity to respond to selection). But it sets up the origin of such correlations, given genetic variation in ornaments and preferences (Fisher 1958; Mead and Arnold 2004; Henshaw and Jones 2020) (Figure 1D).

Second, surprisingly, ornament-preference genetic correlations have seldom been well estimated, in spite of decades of attention. This is because most studies have been severely under-powered (Sharma et al. 2016). Some studies even lacked sufficient underlying genetic variation in ornaments or preferences to allow for the possibility of detecting genetic correlations between them (Fowler-Finn and Rodríguez 2016). Further, the rearing procedures involved in quantitative genetics may often disrupt the correlations they aim to detect (Fowler-Finn and Rodríguez 2016; Hosken and Wilson 2019). Nevertheless, several high-quality studies have reported strong support for Fisherian male-female genetic correlations (Bakker 1993; Gray and Cade 2000; Tallamy et al. 2003; Simmons and Kotiaho 2007; Lüpold et al. 2016). And genetic correlations were more likely to be detected when the required underlying genetic variation was higher (Fowler-Finn and Rodríguez 2016). Thus, it seems premature to reject a potential role for Fisherian selection in evolutionary dynamics with mate choice.

Third, there is a broader framework for ornament-preference coevolution that subsumes Fisherian selection. This is the framework of Interacting Phenotypes and Indirect Genetic Effects (Moore et al. 1997; Wolf et al. 1998; Greenfield et al. 2014; Bailey et al. 2018; Rodríguez et al. 2018). This framework contemplates how social interactions influence phenotypic variation and covariance. The framework brings the key insight that individual phenotypes (say, an ornament or a preference) have components of variation that arise from the bearer's genotype and environment (the direct components), and they also have components of variation that arise from the genotype and environment of other individuals with whom the bearer interacts (the indirect components). The evolutionary consequences of this trait architecture depend on the strength and sign of the inputs into trait variation. Importantly, the consequences include sustaining evolution with no direct genetic variation in traits (because the response to selection may be fueled by the indirect genetic components). They also add strength to a key feature of sexual selection: the cause of selection (the social environment composed of competing and choosing individuals) coevolves with the target of selection. These dynamics may give rise to ornament-preference runaways due to the indirect components of genetic variation, which may in turn give rise to runaways due to the direct components of variation (Bailey and Moore 2012; Rebar and Rodríguez 2015; Bailey and Kölliker 2019).

With a role for subjective experience in mate choice, the dynamics that arise from between-individual interations, with their direct and indirect inputs into trait variation, may be all the more likely and powerful. Further, ornament or preference variants arising from learning and experience may engage the evolution-promoting effects of plasticity, whereby novel phenotypes expose genetic variation in the mechanisms that regulate their expression to selection (West-Eberhard 2003, 2005; Suzuki and Nijhout 2006; Renn and Schumer 2013).

CONCLUSION

Mate choice is so widespread in nature and takes such a broad variety of forms that the explanation for its evolution must be very simple or hopelessly complex. The view of mate choice as a default condition of sexual reproduction highlights the role of competition to engage the discriminating mechanisms that regulate engagement with potential mates. These mechanisms may often involve subjectively-experienced aesthetic evaluation. The project of testing for a sense of beauty in animals will reveal new information on how mate choice is actually expressed in nature, and it will help understand the special features of sexual selection due to mate choice — its power to generate ornament variety and exaggeration, and rapid evolution.

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TABLE 1

Features of sexual selection that distinguish it from natural selection as a cause of evolution (from West-Eberhard [1983, 2014]), and the contributions that the sense of beauty may make towards them.

A: **special features of sexual selection**	**B:** **contribution of sense of beauty when mate choice is the cause of sexual selection**
no optimum, unending change	increases ways to improve on attractiveness; helps fuel response to selection
selective environment evolves with target of selection	
constancy of selection	
advantage of novelty per se	helps explain why novelty is advantageous; increases number of ways to create novelty
strength of selection	increases distance between peak beauty and rock-bottom distastefulness
potential for runaway change	increases the number of inputs that can initiate and sustain runaway change

Figure legend

FIGURE 1. HEURISTIC MODEL FOR HOW MATE CHOICE ARISES AS A LOGICAL CONSEQUENCE OF SEXUAL REPRODUCTION.

Most sexually reproducing species require powerful mechanisms to generate and sustain intimate sexual interactions (especially but not exclusively internally-fertilizing species). Because of the widespread sexual dimorphism in the function that relates reproductive success to mating success, those mechanisms must be sexually dimorphic: Both sexes must be strongly motivated to engage with mates, but the sex with the shallower function must be more discriminating to keep its number of matings near optimum (A). The sex with the shallower function is always selected to remain descriminating, regardless of how much increase there is in the overall attractiveness of the suitors. This necessarily generates competition between one sex (predominantly males) to activate the reward mechanisms in the more selective sex (predominantly females) (B). Variation in the ability to activate these mechanisms necessarily results in mate choice (C). Ongoing mate choice favoring exaggerated ornaments may help establish ornament-quality, as well as ornament-preference correlations (D).