

# Sexual Selection, Aesthetic Choice, and Agency

Hugh Desmond

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## Abstract

Darwin hypothesized that some animals, when selecting sexual partners, possess a genuine “sense of beauty” that cannot be accounted for by the logic of natural selection. This hypothesis has been notoriously controversial. In this chapter I propose that the concept of agency can be useful to operationalize the “sense of beauty”, and can help identify the conditions under which one can infer that animals are acting as (aesthetic) agents. Focusing on a case study of the behavior of the *Pavo cristatus*, I identify the types of evidence that would allow for the inference of agency through aesthetic choice.

## 1. Introduction

When the peahen mates with the peacock with the most adorned tail, what is the best explanation of this apparent choice? The standard way of reasoning about this phenomenon is that the peahen has come to view adorned tails as *a fitness signal*, indicating the presence of a favorable genetic mix. Peahens who are attuned to beautiful tails select better mates, and are able to have a larger number of offspring and/or grand-offspring. However, is it also possible to take the phenomenon at face value? Does the peahen choose the adorned tail simply because it in some sense “believes” the tail to be beautiful? Is the peahen attuned to beauty in the way that humans seem to be?

While the latter view may seem rather folkbiological, it is not clear it can be easily dismissed. When Darwin himself reflected on the sexual display of birds, he wrote this remarkable passage:

Sense of beauty -- This sense has been declared to be peculiar to man. But when we behold male birds elaborately displaying their plumes and splendid colours before the females, whilst other birds not thus decorated make no such display, it is *impossible to doubt* that the females admire the beauty of their male partners. (Darwin 1871a, 1:63, my emphasis)

In this, and many other passages which will be discussed later in the chapter, it becomes apparent that Darwin takes an uncomplicated and even naïve view of the sense of beauty in birds: some birds genuinely appreciate beauty. It would seem that he believed that the complexity of shapes and colors in the peacock's tail could not be adequately understood as only a fitness signal.

What makes this passage remarkable is not just the actual content of Darwin's view, but also the certainty with which he held it, as evidenced in his turn of phrase "impossible to doubt". This is very peculiar and even uncharacteristic of Darwin, who otherwise is so careful in lining up evidence in support of a conclusion that is even then couched with caveats and nuance. There is an element of assertiveness, even certainty in his turn of phrase here. It is reasonable to enquire what the precise grounds – empirical or theoretical – are for Darwin's conclusion. What is the exact evidence that would force the observer to conclude that peahens possess a genuine sense of beauty? Darwin himself does not seem to be explicit about this.

While the phrase "impossible to doubt" reveals some type of epistemic brittleness, rather ironically one could even say that in the 20<sup>th</sup> century it has been "*imperative to doubt*" that some birds possess a genuine sense of beauty! The ornithologist Richard Prum colorfully describes how "Today, Darwin's notion of an aesthetic science of mate choice is treated like a crazy aunt in the evolutionary attic. She is not to be spoken of." And in the 20<sup>th</sup> century, many alternative explanations have been pursued, the handicap principle first and foremost, which explains the peahen's preference as an adaptive trait to the presence of costly and hence honest signals (Zahavi 1975; Grafen 1990a; 1990b; and see recent review in Penn and Számadó 2020). In such theoretical frameworks, there is no such phenomenon as the female choice for the beautiful: there is merely an *apparent choice* for the *apparently beautiful*.<sup>i</sup>

This chapter does not aim to swim against this current, and will not take a definitive stand on whether some species possess a genuine sense of beauty. Rather, my goal is to investigate what conditions would allow attributions of a sense of beauty. This means starting from "Darwin's intuition" that some non-human animals have a

genuine sense of beauty and working backwards to enquire what (1) ontological assumptions and (2) empirical evidence would be needed to *justify* an inference of a genuine sense of beauty.

I will proceed as follows. In the second section I will examine some more textual evidence from *The Descent of Man* to establish what precisely Darwin's intuition was about the sense of beauty, and in particular I will argue that Darwin's affirmation of a sense of beauty presupposes some concept of *objectivist* beauty. In the third section I will briefly review standard evolutionary models of apparently aesthetic choice: fitness signaling, sensory exploitation, and runaway selection. All these models are relatively abstract, and so in order to better ground the discussion, I will delve into the surprisingly complicated empirical details concerning how Indian peafowl (*Pavo cristatus*) make mating choices. It turns out that the process by which peahens choose which peacocks to mate with, depends on many more variables than are often assumed. In the fifth and final section I will turn from this case study, discuss the strengths and weakness of standard evolutionary accounts with regard to this case study, and will suggest there is some empirical ground for inferring a process of *deliberation* at the level of the individual. In such a process, different traits and different elements of a trait are weighed against each other before coming to a decision. I end with identifying the abstract conditions under which one could infer the presence of *aesthetic agency*: the capacity for making choices that are at least partially guided by aesthetic values.

## **2. Darwin's Intuition on Animal Aesthetics**

Any investigation of what empirical grounds there can be for a "sense of beauty" cannot avoid at least some discussion of what is precisely meant by "beauty". While we can, I believe, avoid engaging with internal debates in aesthetics in too much detail, there is one basic distinction in aesthetics that we must take into consideration, namely that between an objectivist and a merely subjectivist conception of beauty.

This distinction can be stated more precisely as follows. Is "beauty" an expedient shorthand, referring to some psychological state of pleasure or desire on behalf of the beholder? Or is "beauty" a genuinely aesthetic concept, referring either to objective properties (patterns in colors, shapes, sounds, movements) or to an objective standard of aesthetic judgment based on combinations of objective

properties? We could call this question the *aesthetic Euthyphro dilemma*: do we call a trait “beautiful” merely because it is (subjectively) pleasing to a potential mate, or is it pleasing to a potential mate because it is (objectively) beautiful?

This dilemma need not be resolved in the same way for all phenomena. The way we use the word “beautiful” may refer to both subjectivist beauty (pleasure appearing as beauty) or objectivist beauty. Darwin himself seems to have allowed for both in the natural world. Especially when comparing interspecific differences in preferences, Darwin seems to emphasize how different species are pleased by different objects or properties. In this sense we may say that what is “beautiful” for the individuals of some species may not be “beautiful” for individuals of another species.

*In the same manner as various animals have some sense of beauty, though they admire widely different objects, so they might have a sense of right and wrong, though led by it to follow widely different lines of conduct. If, for instance, to take an extreme case, men were reared under precisely the same conditions as hive-bees... (Darwin 1871a, 1:73, my emphasis)*

In this quote, usually the statement about the “sense of right and wrong” is emphasized, in order to then question whether evolutionary theory is compatible with moral realism (this is the “evolutionary debunking arguments” literature, following Street 2006). However, the same passage is important for aesthetics, because Darwin implicitly acknowledges that beetles, humans, and various species of bird need not be attracted to the same traits. Elsewhere, he applies a similar remark to aesthetic judgments of body shape, which seem to vary across cultures:

It is certainly not true that there is in the mind of man any universal standard of beauty with respect to the human body. (Darwin 1871b, 2:358)

The lesson to be drawn from such passages is that Darwin does not hold that all apparent manifestations of aesthetic choice need refer to some concept of objective beauty. With regard to some if not many traits, the “sense of beauty” may simply refer to the capacity for discriminating between desirable and non-desirable objects – a capacity that is moreover manifested differently in different species.

This may be a remarkable cognitive capacity, but if this was all there was to Darwin’s views, they would not be particularly remarkable – nor would they have aroused opposition. There is nothing *aesthetic* about this capacity for discriminating

between desirable and non-desirable objects. We may call it “beauty”, but that is really just a figure of speech or perhaps a shorthand to refer to a psychological state of desire.

However, Darwin seems to believe that, at least in some cases, animals seem to be responding to the *objectively* beautiful. There is a genuinely aesthetic sense of the beautiful involved here: the trait is pleasing to a potential mate *because* it is beautiful. This is where the phenomena regarding animal aesthetics become simultaneously interesting and problematic: interesting because the “sense of beauty” here suggests that there are standards of beauty that do not simply refer to subjective patterns of desiring, but to objective standards that are shared between individuals and even perhaps between species. However, this line of thought is problematic because it seems to insert a non-scientific and rather mysterious concept – a standard of beauty – into what would be otherwise a scientific explanation of animal behavior. This chapter will grapple with this problem. However, first, I would like to offer some textual evidence that Darwin’s position on the sense of beauty was in fact this radical.

The first, indirect line of evidence concerns his choice of language: when describing the preferences of female birds, he uses aesthetic and not psychological terms. He talks about bowerbirds “tastefully” ornamenting the spaces where they attract mates (i.e. the bowers), their plumage being “brilliant” or “beautiful”, and their songs as being “sweet strains”:

The Bower-birds, by tastefully ornamenting their playing-passages with gaily-coloured objects, as do certain humming-birds their nests, offer additional evidence that they possess a sense of beauty. So with the song of birds, the sweet strains poured forth by the males during the season of love are certainly admired by the females (...) If female birds had been incapable of appreciating the beautiful colours, the ornaments, and voices of their male partner, all the labour and anxiety exhibited by them in displaying their charms before the females would have been thrown away; and this it is impossible to admit. (Darwin 1871b, 2:61)

The argument here is that, if Darwin indeed intended the concept of “beauty” to be a mere shorthand to refer to psychological states of animals (pleasure, desire), then he would have in fact avoided potential misinterpretation and have spelled out these aesthetic terms in other more empirical terms. After all, Darwin was someone so acutely aware of the connotations of words that he avoided the word “evolution” in the first edition of the *Origin* in favor of “transmutation” or “descent with modification” because “evolution” (from *e-volvere*: ‘unfolding’ or ‘unrolling’) had progressivist

connotations (Bowler 1975). Hence if Darwin wanted to rule out an aesthetic interpretation of this animal behavior, he would have avoided aesthetic language and would have described such bird traits in terms of directly observable properties (movements, sounds, colors, patterns) or in terms of the psychological effects that such properties seem to have on sexual partners. However, Darwin does not do that, and so it is reasonable to suppose he wanted to convey that it is possible to view such properties of bowerbirds in genuinely aesthetic terms.

The second line of evidence is that Darwin, in some telling passages, seems to explicitly operate with a *species-independent hierarchy* of aesthetic choices. He seems to hold that the aesthetic choices in one species can be compared to and ranked against those of another species. In other words, some species or individuals have a *more developed* aesthetic sense than others. The following passage, even though it is of course phrased in questionably Eurocentric terms, does nevertheless illustrate how, according to Darwin, some non-human animals can have a *more developed* aesthetic faculty than some humans:

The taste for the beautiful (...) differs widely in the different races of man... Judging from the hideous ornaments and the equally hideous music admired by most savages, it might be urged that their aesthetic faculty was not so highly developed as in certain animals, for instance, in birds. Obviously no animal would be capable of admiring such scenes as the heavens at night, a beautiful landscape, or refined music; but such high tastes, depending as they do on culture and complex associations, are not enjoyed by barbarians or by uneducated persons. (Darwin 1871a, 1:64)

At face value, these remarks seem at odds with the earlier remarks about “various animals ... admire widely different objects” and the denial of “any universal standard of beauty with respect to the human body”. However, they do not need to be contradictory, because in the passage above Darwin is making a judgment about specific objects (ornaments and music). Not all Darwin’s references to the “sense of beauty” need to be understood in objectivist terms. But Darwin’s ranking of aesthetic faculties only makes sense if he is implicitly operating with some sense of the “objectively beautiful” that grounds such interspecific comparisons and that can be defined independently of how species actually evolved.

In sum, for these reasons I will, for this chapter, assume that Darwin’s intuition on aesthetic choice is that some patterns of mate choice *must* be accounted for as the

mates are being chosen for their beauty *qua* beauty (and not beauty *qua* pleasure). I term this an “intuition” not only because Darwin does not argue explicitly for it, but because phrases such as “impossible to doubt” or “I for one will never admit” convey that his claim has the status of (strongly held) intuition rather than the conclusion of an impassive logical argument. Indeed, his style of argumentation, for instance in the *Origin*, tends towards the inductive and abductive: drawing on multiple lines of evidence in order to put forward the hypothesis that best explains the evidence. However, when it concerns the sense of beauty, he does not weigh various hypotheses potentially explaining mate choice: one is put forward and the others are rejected.

### **3. Three Evolutionary Models of the Sense of Beauty**

It is difficult to take Darwin’s intuition on aesthetic choice – or, at least, my reconstruction of it – as the default option for the apparent sense of beauty among non-human animals. In fact, it was already controversial in Darwin’s own time, being subject to severe criticism from Alfred Russell Wallace. As Jean Gayon notes, Wallace strongly opposed the concept of female choice:

In spite of his usual proximity to Darwin, Wallace perceived [the concept of female choice] as a drift into anthropomorphism, which he considered to be unacceptable. In his view, the notions of beauty, aesthetics and choice were an exclusively human preserve. This criticism highlights an area in which Darwinian tradition borders on the metaphysical... (Gayon and Petit 2019, 82-83).

Gayon also notes elsewhere that this aspect of Darwin’s thought anticipates the later evolutionary thinking of Henri Bergson, who reconceptualized evolution as a creative process and who had some unexpected and under-acknowledged influence on the architects of the Modern Synthesis, including Fisher and Dobzhansky (Gayon 2007).

In contrast to Darwin, Wallace was quite categorical in reducing sexual selection to a special case of natural selection: signals of beauty could be selected for if they correlated with “health, vigor, and general fitness to survive” (Wallace 1878, 211). The peahen selects the peacock with the most elaborate tail not because it “admires” the tail in some genuine sense – i.e., because it meets some standard of beauty or even because it induces pleasure – but because the peahen possesses some

cognitive mechanism that is automatically triggered by certain sensory inputs, in ways that have been shaped by natural selection over the generations.

While it is not the purpose of this chapter to systematically rehearse the rich literature on sexual selection (which also includes the work in ethology in the first half of the 20<sup>th</sup> century), I will briefly sketch three major selectionist hypotheses on animal aesthetics, all of which explain the sense of beauty as a mere “as if” sense of beauty.

### **3.1 Beauty as Fitness Signaling**

The first approach further develops Wallace’s insight, namely that the *vera causa* of mate choice is natural selection: the displayed trait correlates with some other trait that directly improves fitness (e.g., physical strength, parasite load, strength of immune system). This is then why a mating preference that favors individuals with such display traits will itself be favored by natural selection.

One of the challenges for this model is that it entails that dishonest individuals could display the attractive trait *without* the underlying fitness advantage. Such dishonest individuals would be equally successful in attracting mates – and thus, paradoxically, would have equal fitness (in the sense of expected offspring number) as those individuals with physical strength, a good immune system, etc. However, as the strategy of dishonesty proliferates, the mating preference for the attractive trait would itself be decreasingly favored by natural selection. Thus, a fitness signaling model would need to theorize the co-evolution of mate preferences and display traits in such a way that it would lead to a stable equilibrium.

The most well-known resolution of this problem is the handicap principle (following Zahavi 1975), which can be paraphrased thus: only signals that both indicate high fitness *and* that are costly to the individual can qualify as an attractive signal. The underlying rationale of the handicap principle is that attractive traits signal fitness in the same way that conspicuous consumption signals wealth: they are so wasteful that their cost cannot be borne by deceptive individuals and only by individuals who actually do possess the underlying advantage.

For the later discussion, it is interesting to note that Zahavi explicitly took the evolution of the peacock’s tail as exemplifying the handicap principle:



The excessive tail plumes of the peacock which seem to attract the females are obviously deleterious to the survival of the individual. The more brilliant the plumes the more conspicuous the male to predators, and the longer the plumes the more difficult it may be for the male to escape predators or to move about during everyday activity. Hence, only the best males would be able to sustain the handicap. (Zahavi 1975, 211)

For future reference, readers here should note how Zahavi posits a simple causal relationship between the costly trait and ecological activities: the brilliance of plumes is directly related to predation rate. In a later section, we will delve into the empirical literature on mate choice by peahens, and there it will become apparent how complex actual mate choices are and how they resist either generalization or explanation by simple causal relationships.

Zahavi's verbal model has been subject to much discussion, and there are a number of unresolved questions, such as are all sexually attractive traits explainable as handicaps? (Penn and Számádó 2020) There have also been considerable fine-tunings of the main idea: e.g., the hypothesis that high quality males pay a lower cost for the same ornamental signal than low quality males (Grafen 1990a; 1990b). We do not need to delve into this further. What we can take from this short exposition is simply that the presence of a sexual preference for some apparently aesthetic trait can potentially be explained through a process of natural selection of that preference (over other preferences in the ancestral population).

### **3.2 Beauty as Sensory Exploitation**

Another process by which display traits can evolve, is by adapting to pre-existing sexual preferences. A specific way in which this can happen is through sensory exploitation (Ryan 1990): the ornament – or in general, the trait or behavior that attracts mates – is shaped by natural selection to mimic sensory inputs that will cause the potential mate to behave in such a way that the reproductive act becomes more likely.

As an example, consider the mating behavior of water mites (*Neumania papillator*). Males vibrate in order to attract mates (Arnqvist 2006). The reason for this is that water mites (both female and male) hunt for prey by sensing vibrations in the water and then relocating towards the source of those vibrations. On sensing the likely presence of a female (via chemoreception), male water mites vibrate their legs,

thus activating the female's behavioral mechanism for predation, who orients herself towards and starts clutching at the male. Males then deposit spermatophores in front of the female, and continue to fan water towards them. Once females sense the pheromones coming from the spermatophores, they go and pick them up (Proctor 1991, 591). Heather Proctor, in her two studies of water mites, found additionally that (1) male water mites vibrate at the same frequency as copepods, the typical prey of water mites, and (2) well-fed females respond much less to the vibration courtship than hungry females (Proctor 1991; 1992).

This is sensory "exploitation" in the sense that males exploit pre-existing female sensory pathways. Pre-existing preferences are comparable to *exploitable resources* in the social environment. How precisely does this give rise to a selectionist explanation of the evolution of display traits? Initially, the (female) preference is not part of the selective environment. However, once some males evolve another mechanism for exploiting some female preference, the selective environment shifts to include the latter variable (Desmond 2022). The males with the capacity to exploit pre-existing female preference have higher fitness than those who do not. The apparent female preference for males with that capacity over males without that capacity can be fully explained by the features of the selective environment.

Sensory exploitation also offers an alternative approach to explaining the peahen's preference for colorful peacock tails. On this approach, the peahen prefers such tails not because they convey any fitness signal, but because the tail is an adaptation designed to exploit the peahen's sensory-hedonic pathways. For this hypothesis to work, the peahen would need a pre-existing pleasurable response to the sight of color – something that could have adaptively evolved, for instance, to reward a successful perception of colorful fruit. In this selective environment for peacocks, then, peacocks with colorful tails would exploit this hedonic mechanism, allowing for more frequent copulation. The colorful tail is a byproduct of the selection for the perception of colorful fruit. This type of explanation of (apparent) aesthetic preference as sensory exploitation has been generalized to all sorts of aesthetic phenomena, including human music.<sup>ii</sup>

### **3.3 Beauty as Arbitrariness**

In a third important evolutionary model of the apparent sense of beauty, preferences and displays are decoupled from other components of fitness, and individuals may come to prefer to mate with individuals carrying what are called “arbitrary traits”. A rough, intuitive understanding of arbitrary traits is that they are traits that are desired because they are *signals of desirability* – even though they convey no information about other fitness components.

The evolution of arbitrary traits is described by Fisher’s runaway model (Fisher 1915), which goes roughly as follows. Once the preference for a particular type of male trait is sufficiently widespread among females – perhaps merely through drift -- a runaway process can occur. A female choosing a male with the “attractive” trait will likely have sons that have inherited that trait. These sons, in turn, are desired by other females, thus raising the likelihood of a larger number of grandchildren than if she were to mate with a male without the “attractive” trait. The female offspring and grand-offspring inherit her preference for this particular type of male, thus leading to a further spread of that preference in the population. This is why the runaway model is also called the “sexy son hypothesis”: females choose males who are likely to produce “sexy” (attractive) sons, since these are likely to generate a larger number of grand-offspring for the female compared to non-sexy sons.

On this model, the “attractive” trait need not be correlated with other components of fitness. The “sexy” son may be less healthy or vigorous or may be riddled with parasites. However, in the biotic environment where female preferences for that attractive trait are widespread, the “sexy” son has high fitness (i.e., expected offspring number). Hence the epithet “arbitrary”: a trait is desirable because it is seen as desirable, and not because of any other advantage the bearer of the trait may possess. Once preferences and display traits have co-evolved, the desirable trait becomes a signal of desirability.

Richard Prum has proposed that the runaway model, and in particular its further formalization by Lande (1981) and Kirkpatrick (1982), is a candidate for how the sense of beauty may have evolved. In this view, all animals by default possess subjective sensory experiences, and arbitrary traits simply reflect these subjective experiences: the peahen chooses peacocks with elaborate tails not because of implied fitness or because they are being manipulated by peacocks, but because peacocks elicit a subjective experience of beauty. Thus, for Prum, the runaway mechanism is a definite

alternative for functionalist explanations of apparent beauty, and is thus a potential grounding for Darwin's intuition.

Although engaging seriously with Prum's views would deserve a separate paper, I would like to suggest that the runaway model is not necessarily a good ground for an objectivist sense of the beautiful ("Darwin's intuition"). What the Kirkpatrick-Lande mechanism (or Fisherian runaway) describes is akin to a *fashion* trend, or a *herding* process: a self-reinforcing process where desirability grounds itself. And the trait that comes out as the winner in such a runaway process need not be either beautiful nor even pleasing. Examples from human evolution come readily to mind, where adornments have appeared of questionable aesthetic value but causing definite pain and suffering, for instance the binding of the feet of upper-class women in historical Chinese societies, or the use of large lip plates in various indigenous tribes (an example of this is also discussed by Darwin in (Darwin 1871b, 2:341)). Moreover, these display traits (bound feet, or lip plates) were also status signals, and may have been perceived as signals of desirability not because of their beauty in any objectivist sense, but because of their association with high-status members of society. Of course, one could hold that *for those communities* these traits were genuinely viewed as beautiful, and this is exactly the lesson to be taken from this short discussion of the Fisherian runaway process. The runaway process is not constrained by aesthetic standards, and allows, in principle, even the "ugliest" trait to become a symbol of desirability. The runaway process describes self-reinforcing sexual fashions in evolutionary lineages, and at most can account for a subjectivist concept of beauty, and allows for the sense of beauty to be a mere "as if" sense of beauty.

#### **4. Mate Choice Case Study: *Pavo cristatus***

In order to evaluate how well these models can explain apparent preferences among non-human animals for what we might call "beauty", it is important to look in closer empirical detail at how mating choices are actually made within a particular species. Darwin himself considered the patterns of the plumage of the male Great Argus, as well as its displaying behavior, to be one of the most compelling cases for the existence

of a non-human sense of beauty. However, there have been few systematic studies of the exact conditions under which females choose mates in this species. By contrast, the mating behavior of the *Pavo cristatus*, or Indian peafowl, has been studied in much greater quantitative detail. So this section will (non-systematically) review the state-of-the-art of the literature on peahen mate choice in order to add concrete detail to guide the further discussion on the sense of beauty.

***Are elaborate tails preferred?*** “Elaborate” can be operationalized along different variables. One variable is the number of eye-spots on a peacock’s tail: an early study observed that this variable was positively correlated with the number of times that a male would mate in a season (Petrie, Tim, and Carolyn 1991). Another variable is train length (the length of the longest fish-tail feather: another study (Yasmin and Yahya 1996) observed that also this variable was positively correlated with mating success. A third variable is eyespot density: a third study found a positive correlation between eyespot density and mating success (Loyau, Jalme, and Sorci 2005). As a first indication of the complexity involved in charting peahen preferences, this study contradicted Yasmin and Yahya 1996, and found mating success to *negatively* correlate with train length. Nonetheless, while these three studies came up with different results, on the whole they do underwrite the view that “elaborate” tails are consistently preferred by peahens, whether elaborate is understood in terms of eyespot density, number of eye-spots, or train length.

However, even this broad generalization has been challenged. In a 2008 study, Mariko Takahashi and collaborators observed a population of between 75 and 104 peafowl for a period of 7 years – a longer period of time than in the other studies – and they did not find *any* property of the peacock train that predicted mating success (Takahashi et al. 2008). They also reviewed the literature on whether train length was correlated with direct fitness costs: probability of predation, ectoparasite loads, male weight, immunocompetence. For each one of these components of fitness, they found contradictory studies on whether or not train length correlated with those components (see Takahashi et al. 2008, 1215). With that they also cast doubt not only on whether elaborate trains were preferred, but even on the idea that an elaborate tail could be considered a handicap.

How then did the elaborate trains of peacocks evolve, if not by sexual selection? Here Takahashi et al. proposed a non-selectionist explanation: the possession of an elaborate tail is the *default* trait for the *Pavo* genus, hence inherited across *Pavo*

species as a homologous trait, and there is selection for the duller coloration of females. Plumage is colorful by default; the selected trait is dullness. They argued that this is supported by developmental considerations, such as the indications that colorful plumage in peacocks is inhibited by high levels of estrogen. Without active inhibition, colorful plumage develops by default. This study by Takahashi et al. implies a skeptical take on the sense of beauty in *Pavo cristatus*: not only is there not any female choice for beautiful males, but there may not be any female choice present at all, whether for beauty or for fitness signals.

While this study provided an interestingly skeptical counterpoint, further commentaries (Loyau et al. 2008) pointed to crucial limitations and mistaken assumptions in Takahashi et al.'s study. For instance, the size of the peafowl population they studied was lower than that of populations considered by other studies. Moreover, mating preferences are, in general, not species-wide fixed universals, but plastic traits that are sensitive to changing environmental conditions (see also Ryan 2021, 5). So Loyau et al. point to the possibility that the preferences in the Japanese population studied by Takahashi and collaborators developed in different ways due to differences in environment, compared to how preferences developed in the UK population studied by Petrie and collaborators.

Perhaps the most important consideration is that, while it may indeed be wrong to hypothesize that peahens prefer “elaborate” tails, there does seem a preference for *some* combination of traits. Mating success is very variable among peacocks, with many peacocks rejected by all peahens, and some highly preferred. In fact, the most successful males consistently – season after season – carry out a large percentage of all the matings. This is a pattern that is robustly confirmed across lekking species (Loyau et al. 2008, e6). Some peacocks are evidently dramatically more preferred than others. So even if it is not true that peahens simply prefer those with the longest tails or those with the most eyespots, peahens seem to exhibit *some* relatively stable constellation of preferences and are hereby picking up on *some* signals. Even though it is surprisingly difficult to figure out just what these signals are, the precise nature of peahen choice remains an explanandum. Loyau et al. point out that Takahashi et al. did not control for additional quantitative properties that characterize a peacock's train and that could have influenced peahen choice. Peahen choice likely depends on multiple signals. Loyau et al. (2008) mention six properties that characterize peacock trains: three that Takahashi et al. tested for (number of eyespots, eyespot density, train

length) and another three they did not test for (train symmetry, eyespot coloration, eyespot iridescence). The implication is that peahens in the Japanese population observed by Loyau et al. might have been picking up on one or multiple of these latter properties.

***What exactly do peahens prefer?*** Follow-up studies have been helpful in charting a more precise picture of the structure of peahen preferences. One of these (Dakin and Montgomerie 2011) set out to replicate one of the early studies (Petrie and Halliday 1994) and to investigate why Takahashi et al. found a contradictory result. They found that Takahashi et al. were correct in observing that “small” variations in eyespot number do not have a significant impact on mating success; however, once 20 eyespots are removed experimentally, mating success declines drastically compared to that in the control group (see Figure 1). In this way, Dakin and Montgomerie found that there is a cut-off threshold for “acceptable” eyespot count, where 90% of peacocks have 144 eyespots or more. More eyespots does not necessarily increase mating success, and the overall correlation between eyespot count and mating success may be close to zero, but having an abnormally low eyespot count seems to be a cause for *rejection* by peahens.

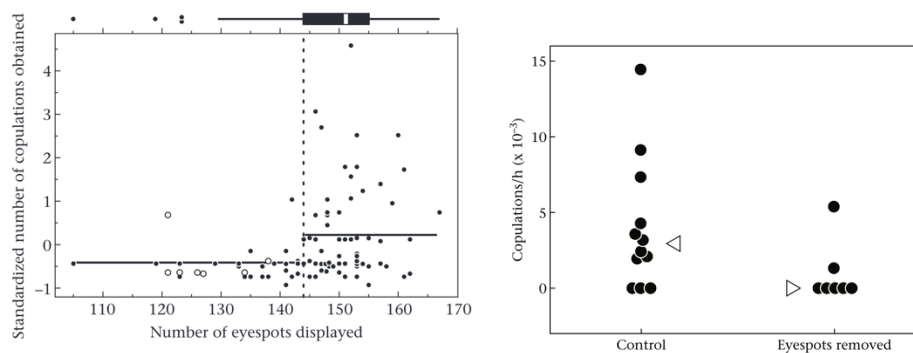


Figure 1: : Peacock mating success mapped against number of eyespots. Figure 1a (left) documents mating success following the manipulation of eyespot number. Figure 1b aggregates data (N=102) from four studies (Dakin & Montgomerie, 2011; Loyau et al., 2005; Petrie et al., 1991; Petrie & Halliday, 1994). It illustrates two regimes of sexual selection, one below a cut-off where mating success approximates zero, and one where mating success is highly variable. The distribution of eyespots is represented in the box plot above the graph. Reproduced with permission from (Dakin & Montgomerie, 2011)

In a series of publications, Dakin, Montgomerie and collaborators charted the role played by other train properties. In one study, they found that peacocks tend to try to face the Sun when displaying their trains, suggesting that peahens respond to the colors and iridescence in the tail (Dakin and Montgomerie 2009). They explicitly tested the role that eyespot color plays in peahen choice by directly manipulating the eyespots in two experimental groups, putting white stickers on the purple-black and blue-green areas of the eyespot tails in one group (see Figure 2), and black stickers on the same area in the other group. What they found was that the mating success in both groups was reduced to almost zero (there was just one peacock in the black-sticker group that copulated just once). The black-sticker peacocks were visited by peahens at the same rate as the control group (but subsequently rejected), whereas the white-sticker peacocks were visited at a lower rate. To human observers, the white stickers were much more noticeable than the black stickers, suggesting that the peahens did not even inspect the peacocks from close by, since they were able to perceive from a distance that normal coloration was absent. Here we seem to have another relatively robust generalization on peahen preference: normal eyespot coloration is a necessary, but not a sufficient condition for a peacock to be accepted by a peahen.



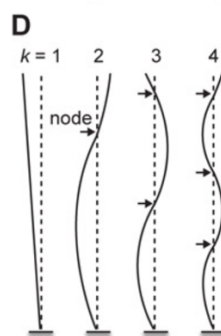
Figure 2: The structure of a peacock eyespot, with three color zones: purple-black (PB), bronze-gold (BZ), and blue-green (BG). Reproduced with permission from (Dakin and Montgomerie 2013).

While it seems safe to say that peahens prefer males with a minimum number of eyespots, and that they prefer the presence of blue-green coloration in the eyespots, these two variables do not precisely predict which individuals tend to be preferred by peahens. For instance, as illustrated in Figure 1, a peacock with an abnormally low eyespot count may have more successful copulations than a peacock with a much



greater eyespot count. The suggestion is once again that there are other, uncharted signals that peahens pick up and that influence their decision.

Dakin et al. (Dakin et al. 2016) investigated the role of behavior – i.e., dynamic properties of strutting, shaking, and solar orientation versus the static properties that define the tail (train length and symmetry; eyespot number, density, coloration, and iridescence). In particular, when displaying their trains, peacocks vibrate the feathers at a frequency of about 25Hz. This exact frequency of train feathers is one of the resonance frequencies; in fact, it is a resonance frequency (mode  $k=3$ ) where the eyespot remains relatively stationary. Dakin et al. hypothesize that the behavior of train vibration thus enhances the attractiveness of the eyespots, since at mode  $k=3$ , the eyespots remain relatively fixed against a dynamic background. This understanding of the potential display function of train shaking addresses one feature of peacock mating behavior that Darwin himself seems to have been puzzled by: “the vibratory movement apparently serves merely to make noise, for it can hardly add to the beauty of their plumage” (Darwin 1871b, 2:61). However, to what precise extent this behavior is in fact a mechanical enhancement of sexually attractive features, and to what extent it influences mating success, seems to be as of yet unknown.



*Figure 3: Vibration of feathers at the various resonance frequencies. The vibration of tail feathers at the various resonance frequencies. Reproduced from (Dakin et al., 2016).*

Let us draw some global lessons from this discussion of the surprisingly complex subfield of peahen mating preferences. First, the question “do peahens prefer peacocks with more elaborate tails” is too vague: a peacock’s tail can be elaborate in different ways, and the overall trait of “elaborateness” needs to be analyzed in terms of component properties to adequately chart which features influence peahen

decisions. Instead of asking an overall question about preference, we first need to be able to identify the exact cues that peahens respond to. Some generalizations seem to be possible here: some cues (minimal eyespot count, the presence of blue-green eyespot coloration) do influence peahen choice. However, none of these cues predicts peahen acceptance. Very conspicuous and abnormal coloration does seem to disqualify peacocks from mating entirely (e.g., covering eyespots with white stickers), but as long as a peacock remains within the statistical bounds of normality, no single cue seems to push peahen choice in one direction or the other.

And this will be the most important lesson that we will draw from this literature. First, peahen choice seems to be present. Some peacocks achieve dramatically greater mating success than others. An illustration of this is reproduced in Figure 5, showing how one peacock seemed to be consistently preferred, suggesting that this did not come about through random mating. However, why precisely the peacock was consistently preferred was not discovered, and that brings us to the second lesson we will draw from the preceding discussion: peahens seem to be picking up on some unknown cues or some unknown combinations of known cues.

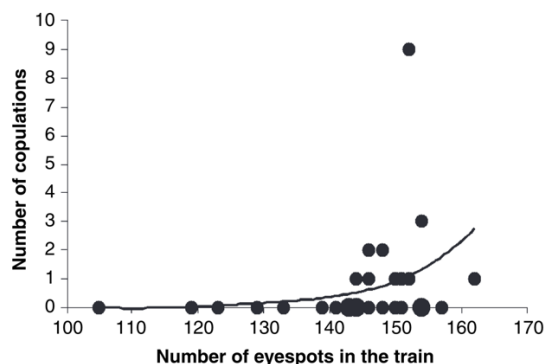


Figure 4: Peahen choice: one peacock (in a population of 34 territorial males observed for about 5 weeks) copulated 9 times – triple the number of times than the second most popular peacock. Reproduced with permission from (Loyau et al., 2005).

## 5. The Conditions for Inferring Aesthetic Agency

To situate the explanatory work done by agency, let us first restate the explanatory rationale for female choice with some more precision. The mechanism of sexual selection was posited to explain the evolution of certain elaborate traits that are too

complex to have plausibly evolved through a drift or random mutation alone, but that do not seem to confer any immediate fitness value, at least relative to the usual ecological goals of nutrition, predator-avoidance, or competition with conspecifics. Female choice – a particular type of sexual selection posited by Darwin – explains the evolution of such traits.

Explanandum: the evolution of elaborate courtship displays (patterns of colors and shapes) and behaviours (dance, song) of males

Explanans: female choice for beauty

Rival evolutionary hypotheses – the handicap principle, sensory exploitation, and runaway selection – offer alternative explanantia for the same explanandum. Such explanations concern the *evolutionary process* (or mechanism) which produces elaborate courtship displays and behaviors that we (human observers) then may judge as “beautiful” in some sense.

The focus of this chapter has been subtly different. It did not concern the evolution of courtship displays, but rather the patterns of manifested female preferences. These empirical patterns are the primary explananda:

Explanandum: actual female preferences, as manifested in patterns of copulation, for courtship displays and behaviors that humans judge to be beautiful

Explanans: female choice for beauty

The same rival evolutionary hypotheses – the handicap principle, sensory exploitation, and runaway selection – offer alternative explanantia of the same explanandum. If these explanantia (i.e., the selectionist hypotheses) turn out to explain the empirical data better, then we must conclude that female choice for beauty is explanatorily dispensable – that the sense of beauty is a mere “as if”. In that epistemic scenario, we should conclude that females *merely apparently choose beauty* and in fact that some other cognitive process explains the behavior.

The disambiguation between these two explanatory schemes – the first an evolutionary explanatory scheme, and the second a cognitive-behavioral one – may strike some as tending towards the pedantic. However, because the schemes share the same explanantia, they are easily confused. In fact, in the literature on sexual selection

the evolutionary explanation has often been interpreted as adjudicating whether female choice for beauty actually exists. For instance, the question of whether or not the handicap principle can explain the evolution of traits such as the peacock tail is often taken to decide on Darwin's intuition about the sense of beauty. However, in determining whether some animals possess a sense of beauty, more fine-grained empirical data is needed (i.e., about the actual behavior of the animals) *alongside* some conceptual clarification of what "beauty" actually should mean in ethology.

In this section I will propose a new way of conceptualizing female choice for beauty: *aesthetic agency*. Using the concept of agency helps clarify why neither sensory exploitation nor runaway selection are good ways to account for female choice. In the following subsection I will briefly sketch what is meant by "agency", and then I will discuss two questions:

- Are empirical patterns of female copulation evidence for inferring that peahen choice is *agential*?
- Are empirical patterns of female copulation evidence for inferring that peahen choice is an instance of aesthetic agency?

## 5.1 The basic idea

Peahens exhibit preferences for particular complex combinations of peacock tail traits. What the exact combinations are that peahens tend to like or dislike seems to be as of yet unknown to humans. We cannot yet pick up on all the cues that peahens seem to be picking up on. But peahens are not copulating at random with peacocks: certain peacocks are dramatically more preferred than other peacocks. There is some define combination of traits that makes the first group more preferred.

This range of combinations of traits that are preferred by peahens can be called the "peahen standard of beauty". This standard can be posited as accounting for why some combinations but not others tend to be preferred. Why call this "beauty"? First, because the peahen does not seem to be *manipulated* by the peacock. Second, and more importantly, because the peahen does not seem to be passively – "mindlessly" if you will – controlled by some inherited cognitive mechanism that is triggered by certain sights and sounds. She inspects the peacock, takes her time to allow a full range of courtship displays; if interested, she stays to gather more information. There is also no single "magical" property that triggers her interest. The peahen is taking in the

whole trait of the tail – and to some extent, the whole individual peacock as well, since the attractiveness of the peacock also seems to depend on how the peacock struts and shakes its tail. In this sense, it seems plausible to believe that the peahen’s mind is *weighing* the different tail-related attributes – not entirely dissimilar to a connoisseur of art – to come to an informed judgment of whether the peacock tail truly meets her standard of beauty. It is the peahen making the choice, and though the broad contours of her choice are surely shaped by a selectionist history (e.g. the types of sensory input she finds pleasurable), her behavior is not being controlled by natural selection.

Why call this “beauty”? Not just because the peahen seems to be actively choosing which peacock to mate with, but because neither fitness nor sensory pleasure seems to entirely account for how the peahen makes her choices. An evolved sensory-hedonic pathway of the peahen may produce pleasure at the sight of certain colours – but the mere presence of such colors is not sufficient to trigger peahen acceptance. Certain tail shapes and sizes may indicate underlying fitness advantages (per the handicap principle), but the mere presence of such a fitness signal is again not sufficient to trigger peahen acceptance. Pleasure and fitness may be reasons to *reject* some peacocks – and peacocks who lack sufficient eyespots or who lack the standard blue-green coloration are widely rejected by peahens. However, there is some extra cognitive processing going on. Peahen acceptance depends on finer-grained distinctions between combinations of colors, shapes, sounds, and movements that seem equivalent in fitness or even activation of re-existing hedonic pathways.

Yet, one could insist why then call this “beauty” rather than idiosyncrasy? In this last step, some anthropomorphic element comes in. We call this a standard of beauty, because humans also judge the preferred tails to be beautiful. And insofar as there is evidence that peahens have a structurally similar cognitive ability to make fine-grained but definite judgments about what they prefer, there seem to be good grounds for categorizing this cognitive ability as a form of *aesthetic choice*.

## **5.2 Agency**

The term “agency” is used across so many different contexts – philosophy of action, phenomenology, ethics and politics, and increasingly, ecology and evolution – in a variety of ways. Overwhelmingly, agency is taken to refer to a capacity of *goal-directedness*, not just in humans (agency as intentionality) but also in non-human

animals (e.g. Walsh 2015). However, this is not how I will be using the term. I understand agency to be a rival explanatory principle to natural selection, where the trait or behavior of an organism is explained through the action of the organism itself, instead of through the action of a long and gradual process of evolution by natural selection. In other work (Desmond, ms.), I have argued that it is insufficient to take goal-directed behavior as evidence of the presence of agency, since goal-directed behavior (e.g., functionality) can in many cases also be well explained by natural selection. Instead, agency is better captured by the “deliberative model”. Agency should be thought of as a process of *deliberation*, where *multiple* goals are weighed against each other, and where the *choice* of a particular course of action occurs at the level of the organism.

Technically, I show how this idea can be formalized as a form of symmetry breaking in the selective environment. The selective environment determines the stable goals for the organism, but these goals are symmetries for actual behavior. In other words, it is not to say that nutrition, or mating, or predation avoidance is the “most important goal” without any further qualification. All are crucial for the overall fitness of an organism. However, in particular environmental circumstances that do not feature in the selective environment, one goal may need to be prioritized over others: this is symmetry breaking, and “agency” is simply the concept that captures the organism acting to break the symmetries in the selective environment.

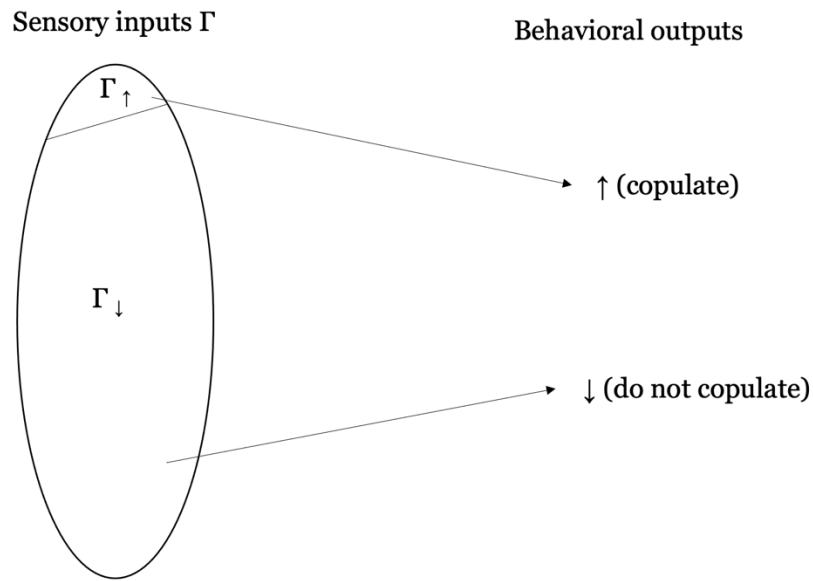
The upshot of this agential approach is that decisions about whether an animal possesses a “sense of beauty” are not decided by questions of whether they possess a certain type of qualitative subjective experience. “Beauty” is not merely an experience – it is also an *action*. Whether or not a peahen possesses a sense of beauty depends (1) on whether she is making a genuine decision (or choice), and (2) on whether aesthetic properties are one of the significant factors guiding her decision-making.

### **5.3 Does the Peahen Preference Structure Exhibit Agency?**

The first question – is there a genuine decision – I will approach by asking whether the particular preference structure can be explained fully by a process external to the peahen. Since the preference structure seems to be highly designed (e.g., peacocks without blue-green eyespot coloration are rejected), natural selection is a prime rival candidate to explain the preference structure.

Preference structures can be viewed as structures connecting inputs to outputs. In the case of peahen choice, the outputs are simple: accept or reject (i.e., copulate, or do not copulate). The input variables are more numerous. There are at least six visual variables: number of eyespots, eyespot density, train length, train symmetry, eyespot coloration, and eyespot iridescence. Further, there is at least one relevant audiovisual variable: the frequency of vibration of the feathers. Some other audiovisual variables discussed in the literature – the calls to attract attention of females, or the reorientation to face the Sun – matter only insofar as they affect how these seven variables are perceived. Although the full number of variables peahens pick up on is not known, let us just assume for our purposes here that there are seven independent input variables.

Let  $\gamma_1, \dots, \gamma_7$  represent these potentially relevant input variables. Only certain combinations of these variables lead to acceptance. Let  $\Gamma_{\uparrow}$  represent the set of sensory vectors  $(\gamma_1, \dots, \gamma_7)$  that trigger acceptance in the peahen. Then  $\Gamma_{\downarrow}$  represents the set of sensory inputs that lead to rejection. Since peahens are “choosy”, we may assume that  $\Gamma_{\uparrow} > \Gamma_{\downarrow}$ : there are “more” combinations of (developmentally possible)<sup>iii</sup> sensory inputs that lead to peahen rejection than inputs that lead to peahen acceptance. The mapping of sensory inputs onto behavioral outputs corresponds to a partition of the set of sensory inputs  $\Gamma$  into  $P = \{\Gamma_{\uparrow}, \Gamma_{\downarrow}\}$ . This is what I mean by the *preference structure* of the peahen.



$$\Gamma = \gamma_1 \times \gamma_2 \times \gamma_3 \times \gamma_4 \times \gamma_5 \times \gamma_6 \times \gamma_7$$

*Figure 4:* The (sexual) preference of an individual organism may be represented by the mapping of the multidimensional space  $\Gamma$  (consisting of combinations of relevant sensory inputs) onto the space of relevant behavioral outputs. Note that this mapping may differ from individual to individual, even within the same population.

Preference structures need not always be explained as involving deliberation or choice. They can be automatic processes, triggered by certain types of sensory input, and explainable as inherited and shaped by natural selection. Hence, for the explanandum “preference structure  $P$  of organism  $O$ ”, the explanans “preference  $P$  has a higher fitness than  $P'$  in  $O$ 's ancestral selective environment” may be well suited.

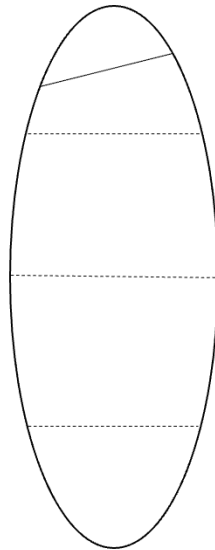
$$w(P) > w(P') \geq w(P'') \geq \dots$$

This is how both the handicap principle and Fisherian runaway selection explain the evolution of mating preference structures. According to the handicap principle, the evolution of preference structure  $P$  can be explained if  $P$  allows the organism to track traits that convey fitness advantages such as health or immune strength in a superior way compared to rival preference structures  $P'$ . According to the runaway mechanism,  $P$  also allows organisms to track traits that convey fitness advantages, but just a different type of fitness advantage: conformity to pre-existing mating preferences.



A more abstract but more fundamental way of restating this is by partitioning the set of sensory inputs into zones of equal selection pressure. Each combination of sensory input corresponds to an implied state in the external environment. Not all variations in sensory input will make a difference to implied selection pressure: for instance, it may not matter for expected fitness whether the predator is close or extremely close. These sensory inputs are “equivalent” from the perspective of fitness: they describe identical states in the selective environment (for a more extensive introduction to the concept of the selective environment, see Desmond 2022; 2021, drawing extensively on Brandon 1990; Levins 1968).

Sensory inputs  $\Gamma$



*Figure 5:* Two ways of partitioning the space of possible sensory inputs. The solid line partitions the space according to behavioral outputs. The dotted line partitions the space according to equal (implied) fitness values following copulation.

The question then is, does the fitness partition of the set of sensory inputs  $\Gamma$  correspond to the preference partition  $\{\Gamma_{\uparrow}, \Gamma_{\downarrow}\}$ ? In other words, do preferences track fitness differences? If they do, then the preference partition can be explained as a property that evolved through natural selection. The preference of the peahen picks up on subtle combinations of sensory inputs that have recurred again and again throughout generations, allowing the shaping of a cognitive mechanism that automatically translates these exact combinations of sensory inputs into behavioral choices. Such a cognitive mechanism would be *domain-specific* and *automatic*. There would be no need to invoke agency to account for the decisions of the peahen. The

decisions of the peahen are not really “its” decisions, but rather – to put it metaphorically – “the decisions of natural selection”. However, if the preference partition does not map onto the fitness partition, then there are grounds for invoking agency. The organism may be more picky than natural selection is, preferring some sensory inputs over other sensory inputs, even though there may not be any implied fitness difference. The organism may also be *less* picky than natural selection, preferring some sensory inputs even though they imply a lower fitness compared to other sensory inputs.

So note that, here, the Lande-Kirkpatrick mechanism does not offer grounds for inferring agency, because the preference partition *does* correspond to the fitness partition. In other words, the choices of individual peahens are determined by the expected choices of *other* peahens, and thus by the expected fitness of the sons, grandsons, and granddaughters of the peahen. The peahen chooses the peacock with the highest expected offspring number. For a preference structure to be considered as agential, preference need not necessarily be manifested for the less fit (such preferences might not be long-lived), but preferences need to be *more fine-grained*. An individual peahen must have its own preferences that may not correspond entirely to the preferences of other peahens.

Are these conditions met in the case of what we know of peahen choice? There is much we do not know of the precise structure of  $\{\Gamma_{\uparrow}, \Gamma_{\downarrow}\}$ , so definitive answers are not possible. However, we do know that (1) a minimum number of eyespots is necessary but not sufficient for acceptance, (2) the presence of the blue-green eye color is necessary but not sufficient for acceptance, and (3) in general, there does not seem to be any single variable which, once it assumes a particular value, can guarantee acceptance. Together they do raise the likelihood that there is no simple domain-specific cognitive mechanism that can be triggered by a threshold input. Peahens seem to evaluate *combinations* of sensory inputs.

It should be acknowledged at this point that there is some good evidence that the peacock tail is *also* an honest fitness signal. Peacocks with a large number of eyespots had low levels of heterophils – a type of white blood cell common in birds – which in turn suggested a more effective immune system or a lower infection rate (Loyau et al. 2005). In *some respects*, the elaborateness of the peacock tail *can* be understood as an honest fitness signal in the way envisaged by the handicap principle; the question is whether the handicap principle *fully* explains how peahens make mate

choices. The preference for the minimal number of eyespots seems to be readily explainable by classic handicap principle hypotheses. However, when we shift the explanandum – why precisely this or that peacock is consistently preferred in a given population – then the hypothesis no longer seems sufficient.

The main skeptical response here is to point to the possibility that the combinations of signals that peahens are picking up on *do* indicate fitness advantages. This hypothesis cannot be ruled out – but here arguments about the burden of proof arise (already raised by Prum 2010). If no evidence exists for combinations of signals that both correlate with fitness and that perfectly determine peahen preference, then it is reasonable to infer that peahens are making a *genuine choice* – and that they are not simply acting as conduits for the “preferences” of natural selection, so to speak.

#### **5.4. Does the Peahen Preference Structure Exhibit Aesthetic Agency?**

If peahens are making genuine choices – i.e., by weighing multiple audiovisual cues, where no single cue by itself can determine acceptance, but where the outcome of acceptance/rejection seems to be based on some standard and is not merely random – the question arises *what standard* is guiding the choice.

Fitness could conceivably be such a standard: this is why the agential model of mating preferences does not imply that displays cannot be fitness signals. The agential model only implies that the individual does not process fitness signals in a way that is entirely determined by natural selection. Thus, an individual may *weigh* different and perhaps contradictory fitness signals, and thus come to a decision on whether to accept or reject a mate.

Whether or not peahens exhibit aesthetic agency depends, first, on whether this weighing of fitness signals can fully explain mate choice patterns. In other words, fitness may be one of the standards guiding peahen deliberation, but can peahen decisions be adequately explained by reference to fitness alone? Thus, a peahen may inspect peacock for a minimal eyespot count because a minimal eyespot number is correlated with the health status of the peacock. However, peahens inspect peacocks for many other properties, and seem to make fine-grained distinctions between very particular combinations of properties that seem to be equivalent according to a standard of fitness.

Pleasure is another standard to guide agential deliberation. According to this standard, peahens choose peacocks that, through their audiovisual displays, elicit most pleasure. Note that this is an agential version of sensory exploitation hypotheses. In sensory exploitation, the male triggers acceptance by the female through manipulating the sensory-motivational pathways of the female. By contrast, in “hedonic agency” (if you will), the peahen is actively deliberating whether the peacock is eliciting sufficient pleasure, may hesitate between different displays that elicit a similar quantity (and/or quality) of pleasure, and finally decide for one particular peacock.

If some combination of the standards of fitness and pleasure could fully explain peahen choice, there would be no reason to invoke “beauty”. To invoke aesthetic agency, one needs to assume some distinction between the concepts of beauty and pleasure – an old and difficult question that we should not pretend to answer in this context. Even the concept of pleasure is more complicated than would seem at first: is pleasure a subjective state that exists only in degrees, or are some pleasures “superior” to others, with aesthetics one of the hallmarks of “superior” pleasure? Think of J.S. Mill’s criticism of Benthamite utilitarianism, and his claim that pleasures arising from the exercise of “higher” mental faculties are superior (Mill 2003, 187–89). For purposes here, we can first assume that sexual choices in virtue of a beauty standard are always accompanied by pleasure: no beauty without pleasure. Second, we can limit the meaning of “pleasure” to simply refer to the stimulation of a sensory-motivational pathway that evolved to signal fitness-enhancing circumstances. Say that members of a species experience pleasure upon seeing a color, because the species evolved a pleasurable response to the perception of certain green, red, or yellow colorations of smallish objects (such as fruit). If then females deliberate on which males best elicit visual pleasure, this is a form of agency that need not be categorized as *aesthetic* agency.

The question thus becomes: can the patterns of stimulation of the sensory-motivational pathways that evolved via natural selection fully explain actual mate preferences? More concretely, as the pleasures of various independent sensory cues are weighed, does the “total quantity” of pleasure determine which mate is chosen, or is there some “other standard” by which the various pleasures are weighed? If the total quantity of pleasure does not determine mate choice, then this is ground for supporting the existence of an aesthetic standard.

Let us focus this question with a specific example: preferences for the ocelli in a peacock tail. Ocelli are very common ornamentations across species, and are thought to have evolved as an anti-predator adaptation: by mimicking vertebrate eyes, ocelli confuse predators (Lönnerstedt, McCormick, and Chivers 2013). One could thus speculate that ocelli may have originally been preferred by potential mates as a fitness signal (i.e., lowered probability of predation), and through preference-display coevolution, the sight of ocelli may at a certain later point (whether for descendent generations or even descendent species) have elicited pleasure. This would be a rationale for construing any agential deliberation according to a hedonic standard.

However, ocelli are composite visual inputs: they consist not just of an eye-like shape with brighter and darker colorations, but also of different hues of green, purple, gold, and so on. The ocelli in some bird species, such as the Great Argus (Figure 7), are characterized by great intricacy. While an adaptationist-hedonic explanation could be entirely adequate for explaining the preference for ocelli in some species (a rather persuasive adaptationist account of ocelli in damselfish is given by Lönnerstedt, McCormick, and Chivers 2013), it is not so clear whether it adequately accounts for a preference for such intricate structures in the plumage of species such as the Great Argus, since similar pleasure (i.e., the stimulation of sensory-hedonic pathways) could be elicited with far simpler structures. The explanans – the standard of pleasure – is not *specific* enough (*sensu* Woodward 2010) to account for the explanandum – the patterning of female choice.

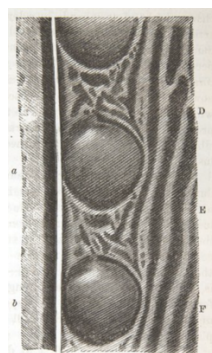


Figure 6: Ocelli in the plumage of the male Great Argus, the complex patterning of which astonished Darwin. Reproduced from (Darwin 1871b, 2:146).

This then helps point to the empirical and epistemic conditions where it becomes justified to infer aesthetic agency: the preference structure is *more fine-*

*grained* than would be expected if only fitness and pleasure were the standards by which courtship displays were judged. Some individuals, such as the females in a number of peafowl species, seem to exhibit preferences for courtship displays that do not seem to differ in fitness signaling, and that seem to equally stimulate any (hypothesized) evolved sensory-motivational-hedonic pathways. In such conditions, it would seem reasonable to conclude that such individuals are influenced by some standard of beauty of their choice. This standard, in the case of many lekking species, seems to overlap with the standards of beauty most if not all humans hold, suggesting the yet more surprising conclusion that some aspects of standards of beauty can, at least to some extent, be defined independently of species. However, the development of aesthetic agency is not necessarily identical across species – and differing standards of beauty may be part of the explanation: thus peahens seem to be far more discerning of “peacock beauty” than humans are, as they evidently exhibit strong preferences for some peacocks over others, where humans would be left indifferent.

## **6. Conclusion**

If anything, the broad current of intellectual enquiry seems have been to use selectionist and adaptationist hypotheses to account for the realm of human art and aesthetics (for a recent review, see Tiège, Verpooten, and Braeckman 2021). However, what if this explanatory direction were to be reversed, and if some animals were considered to possess an aesthetic judgment traditionally reserved for humans? The possibility is fascinating, and has intrigued subsequent generations of biologists since Darwin, but the risk looms that this is mere anthropomorphic thinking. I believe that the concept of agency offers a fruitful path forward, since it pivots the discussion away from the strengths and weakness of evolutionary models (such as the handicap principle), and instead reorients our attention towards explaining actual – and rather noisy – animal behavior. Two questions should be asked when deciding whether some animal species (or a particular sex of a species) possesses a “sense of beauty” with regard to their potential mates: are they making their own, genuine choice among mates (as opposed to being entirely guided by natural selection), and is a standard of beauty shaping this choice (alongside standards of fitness and/or pleasure). Even with regard to how mate choices occur in a species such as peafowl – a relatively easily

observable bird – we are still surprisingly ignorant about what combination of factors determine peahen preferences. However, given evidence that peahens seem to weigh different factors in ways that cannot be obviously accounted for by many leading adaptationist hypotheses, there are grounds for carefully lending at least some credence to the intuition shared by Darwin and many others that, indeed, peahens do have a sense of beauty.

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<sup>i</sup> Note that one should speak of "individual choice" rather than "female choice", since in some species, males are the ones that select which female partners to copulate with. However, this chapter is concerned with the species that offer the best available potential evidence for the existence of the sense of beauty – and these seem to be bird species where the females select which male to copulate with. Hence in this chapter, I will in many places, for sake of simplicity, simply speak of "female choice".

<sup>ii</sup> "I suspect that music is auditory cheesecake, an exquisite confection crafted to tickle the sensitive spots of at least six of our mental faculties." (Pinker 1997, 534)

<sup>iii</sup> An implicit assumption here is that the space of  $\Gamma$  does not refer to all physically possible input values (this would not be a concept that is appropriate for a biological context), but rather to physically possible input values that are in some sense "developmentally possible" within the *Pavo cristatus* lineage.