Richard O. Prum, The evolution of beauty: How Darwin's forgotten theory of mate choice shapes the animal world - and us, New York: Doubleday, 2017, 448 pp., \$30.00 hardback.

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In this book, Richard Prum, Yale professor in evolutionary ornithology, defends a theory of sexual selection in which the act of choosing a mate for purely aesthetic reasons - for the mere pleasure of it - is an independent engine of evolutionary change. Dubbing this process 'arbitrary coevolution' or 'beauty happens', Prum pits it against the good genes model of sexual selection through mate choice. The first two thirds of the book provide an in-depth theoretical discussion of these two models of sexual selection by way of comprehensive, upto-date review of the biological literature on fascinating sexual displays and life of birds such as ducks, bowerbirds and neotropical manakins. Shifting his attention to humans in the final third of the book, he explores how his theory may explain a variety of traits such as the female orgasm (and the intensity of the male orgasm) or 'pleasure happens', reduced physical weaponry of men in comparison to other great apes or 'aesthetic deweaponization', and the evolution of same-sex behavior or the 'queering of Homo sapiens'.

The book has received a fair bit of media attention and was a 2018 Pulitzer prize finalist and named a best book of the year by the New York Times book review, Smithsonian, and Wall Street Journal. This should not come as a surprise as Prum delivers a skillfully crafted account that is provocative, engaging, funny and at the same time informative.

However, academic reception, especially from colleague biologists working in the domain of sexual selection, has been more critical. Prum's colleagues mainly take issue with two fundamental aspects of the book. Concerns have been raised regarding the dichotomy he presents between his 'arbitrary coevolution' theory and good genes, on the one hand, and the portrayal of evolutionary biologists' and psychologists' underlying preferences and ideological biases, which, purportedly, lead them to favor good genes, on the other.

Before delving into that controversy, it is necessary to give a brief account of Prum's main scientific argument. Central to Prum's thesis is 'beauty happens', which is based on coupling runaway sexual selection (or 'arbitrary coevolution' as Prum renames it) to Darwin's proposal that the proximate mechanism of mate choice is the chooser's 'taste for the beautiful' (*The Descent of Man, and Selection in Relation to Sex.* London: John Murray, 1871). The runaway model holds that the process of (usually female) mate choice can create a covariance between

the genes for a given (usually male) display and the genes for the preference for that display. Crucially, it was shown that merely due to this correlation elaborate display traits could evolve even if they lower viability (survival and fecundity) of their bearers. The driver of this runaway process is thus, according to Prum, the females' 'taste for the beautiful' which he considers a product of their 'subjective experiences'. He explicitly contrasts this process with the traditionally dominant good genes model. The good genes model entails that, rather than being arbitrary, the male sexual ornaments on the basis of which females choose, reliably indicate genetic quality of the males.

The dichotomy between subjective arbitrary coevolution and 'objective, informative' good genes runs like a thread through the book. A major argument that Prum makes against good genes is that it rests on unscientific grounds and (past) ideological biases. He claims that common adherence to good genes can be explained by scientists' need "to believe that the world is filled with 'rhyme and reason'" (p. 49) rather than arbitrariness, and therefore they are biased to support the utilitarian and reductionist good genes model. Moreover, he asserts that "some core, fundamental commitments of eugenics were 'baked into' the intellectual structure of evolutionary biology" and that it "did not overcome its eugenic history" (p. 326). I do not think that Prum wants to go as far as to accuse his colleagues of a hidden Nazi agenda, but it might make them look 'guilty by association' in the eyes of this trade book's broad audience. It should therefore not come as a surprise that fellow researchers did not appreciate it. But it also led to some responses that might be interesting from a philosophy of science perspective.

For example, Borgia, one of the leading experts on bowerbird sexual selection research, and Ball (*Animal Behaviour*, 137, 187–188, 2018) responded to this characterization that "science is about understanding what nature is, not what we want it to be". This response testifies to the fact that some scientists still choose to present science as a bastion of unbiased truth (though mainly in popularizing books), despite the fact that philosophers of science have long been arguing that science cannot be entirely value-free. Prum's provocative 'solution' to deal with this issue is to let, not only his opponents', but also his own biases openly play a role in his argumentation, rather than striving for (the appearance of) scientific neutrality. For example, in arguing against good genes, which de facto reduces sexual selection to natural selection, he writes that he has always found natural selection "sort of boring" (p. 11). Remarks like this surely appear dramatically honest and make for entertaining reading. However, unfortunately, it also brings him into a position where he flirts with committing naturalistic fallacies throughout the book. For example, he contests the byproduct hypothesis of the female orgasm because "feminists ... have argued that the by-product hypothesis marginalizes and trivializes the sexual agency of women" (p. 272).

Prum presents himself as a lone advocate of a non-adaptationist account of mate choice, while in reality many other evolutionary researchers take that option seriously. Furthermore, the dichotomy Prum presents between 'subjective' runaway and 'objective' good genes is incorrect on several counts as has also been noted by Patricelli, Hebets and Mendelson (*Evolution*, 73(1), 115–124, 2018).

First, Prum assumes that the role of subjective aesthetic pleasure or desire of females is necessarily linked to runaway/arbitrary coevolution. Yet, there is no reason to assume that

choosing mates based on arbitrary traits is more likely to be mediated by these proximate processes than when choosing correlates with good genes.

Second, the dichotomy presents good genes and runaway as mutually exclusive processes, while they actually may mostly work in concert, as is captured by sexual selection continuum theory. More importantly, the dichotomy ignores other mate choice theories that are generally accepted to play a role as well. In particular sensory bias and sensory drive theories have seen a surge of interest in the last few decades, yet Prum fails to mention them. In fact, arbitrary coevolution is not the only non-adaptive alternative to good genes, sensory bias has been explicitly presented as such as well, for instance in Michael Ryan's recent book on the aesthetics of mate choice (A taste for the beautiful: The evolution of attraction. Princeton: Princeton University Press, 2018). Basically, Ryan's work shows that male sexual ornaments may evolve to exploit female preexisting biases, for example for finding food or avoiding to become food. Interestingly, examples Prum discusses purportedly in favor of arbitrary coevolution are arguably rather in line with sensory bias theory. For example, Prum writes that the evolutionary psychological literature regards facial youthfulness or 'femininity' of women - that is, relatively small chin and large eyes, high cheekbones, and full lips - as an evolutionary indicator of female reproductive value. Yet, Prum notes, youthfulness by itself is not heritable. Therefore, he reasons, "the only plausible response to mating preferences for indicators of youth is the evolution of traits that *lie* about age" (p. 258). Hence, "preferences for [female] facial 'femininity' are excellent evidence that mate choice is not adaptive but arbitrary" (p. 258). I am willing to follow Prum's argument that women who happen to appear younger than they actually are may benefit from the male's evolved preference for youthfulness, even though this might be arbitrary with respect to these women's genetic quality. However, it is clear that this constitutes sensory exploitation rather than runaway coevolution, simply because the male's preference for youthfulness does not require coevolution with these traits. It is merely the case that these apparently youthful women exploit the male preferences for youthfulness for their own reproductive advantage.

This brings us to a similar point of discussion regarding Prum's general aesthetic theory, which he proposes towards the end of the book. Prum states that aesthetics constitutes by definition arbitrary coevolution, arguing that an aesthetic response is always the result of a coevolutionary process. And if that cannot be the case, as with the appreciation of a sunset (the setting sun could impossibly have coevolved with our appreciations), then, according to Prum, this constitutes a 'projection' of an aesthetic response which did result from some previous coevolutionary process. However, the occurrence of such projections is exactly what sensory exploitation kind of models would predict - a projection *is* an incidental byproduct of pre-existing biases or preferences.

Furthermore, Prum tends to ignore the fact that, despite the significant interspecies and individual variation, there are also striking similarities, which cannot be purely coincidental. The subtitle of the book proclaims that the pleasure driven runaway hypothesis Prum presents is "Darwin's forgotten theory about mate choice". Yet, Darwin did not neglect sensory biases as he remarked that "man and many of the lower animals are alike pleased by the same colours, graceful shading and forms, and the same sounds" (p. 93), which might be due to shared "physiological principles" (p. 92). Indeed, these commonalities might point to a universal aesthetic, due to deep homologies in how neural systems work, from insects to vertebrates. This deep homology can account for the remarkable fact that we, humans, find

ornaments shaped by mating preferences of this wide range of species often aesthetically pleasing as well, which is something Prum's theory cannot account for.

The last third of the book Prum devotes to applying his beauty happens/arbitrary coevolution theory to humans. I found this part, just as the first two thirds, entertaining and often informative. For instance, his 'aesthetic deweaponization' proposes that women – just as females of some animal species - have used "aesthetic mate choice to transform, or remodel, males to be less coercive, disruptive and violent" (p. 294). He proposes that "deweaponization is essentially the reduction of male armaments (which have evolved by the process of malemale competition) through female mate choice" (p. 294). Although there are plausible ecological explanations for reductions of male-male contest competition and weaponry, the hypothesis that female aesthetic agency had a major role is intriguing.

However, this part on humans is also overshadowed by the way Prum pictures his opponents. Here the bogeymen are evolutionary psychologists. "Evolutionary psychology is bad science" Prum claims (p. 367) as it "has a profound, constitutive, often fanatical commitment to the universal efficacy of adaptation by natural selection" (p. 226). I am sympathetic to Prum's worry that both evolutionary psychology and evolutionary biology have been generally too generous with adaptationist explanations. However, arguably he discredits the entire field of evolutionary psychology based on a straw-man – or outdated – version of the field.

Ironically, his 'new' ideas are more in agreement with contemporary evolutionary psychology than he seems to realize. For instance, Prum considers it as "one of the more tiresome evolutionary psychology truisms" (p. 254) that men compete and women choose and contends that, because men, unlike other male apes, make substantial reproductive investments (i.e., paternal care), they have evolved to be choosy as well about whom they want to reproduce with, which resulted in the evolution of distinctly female sexual ornaments – like permanent breasts and distinctive body shape. Yet, rather than correcting evolutionary psychology, he is needlessly reinventing the wheel here, as male mate choice and resulting female ornaments have already been acknowledged by evolutionary psychologists (Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior*, 31, 157–175; Stewart-Williams, S., & Thomas, A. G. (2013). The Ape That Thought It Was a Peacock: Does Evolutionary Psychology Exaggerate Human Sex Differences? *Psychological Inquiry*, 24, 137–168).

In conclusion, I much enjoyed reading *The evolution of beauty*, both for its provocative style and the rich body of speculations and observations it contains. Despite my concerns, I regard Prum's take on the evolution of aesthetics thought-provoking and worthy of consideration. And, although the picture Prum paints of contemporary sexual selection research is seriously biased - and he does not try to hide it -, it may help to correct the mainstream view that good genes selection is the only major explanation for the evolution of elaborate sexual displays and ornaments.