



## Book Review

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

For more than 30 years there has been an intensive debate (Bradbury & Andersson 1987) about how elaborate and often-beautiful male display traits evolve. A variety of models have been proposed, nearly all based on Darwin's female choice driving the evolution of male display traits. Richard Prum describes himself as a rare field biologist who views runaway sexual selection as the critical force shaping female choice and male sexual display. One focus of his career has been to study the male sexual displays of neotropical manakins. In this engaging and provocative book, Prum writes about manakins and other avian species with complex and beautiful displays. A major issue addressed is the controversy concerning models that explain the evolution of these elaborate male display traits. He limits this controversy to a dispute between two models, originally suggested by Fisher (1915, 1930): the Lande-Kirkpatrick (LK) version of runaway selection (see Prum, 2010), and adaptive sexual selection, particularly 'good genes' models (e.g. Trivers, 1972). Although abundant evidence exists for good genes and adaptive models of sexual selection, and they have been effectively used to explain female preference for elaborate male displays, Prum denies their importance.

One of Prum's rhetorical tactics is to out-Darwin his opponents. He claims that his views on sexual selection are Darwinian, while good genes advocates embrace the views of A. R. Wallace (1889). Wallace's signature response to Darwin's theory of sexual selection was that female choice does not occur, and that elaborate male display ornaments are expressed as a result of high levels of 'vital energy' and blood circulation in associated male tissues. However, it is now widely understood (e.g. Møller & Alatalo, 1999) that good genes models are based on female choice. Yet in Prum's revisionist analysis, good genes advocates and Wallace were misguided adaptationists, while Darwin, who invented making adaptive predictions from selection theory, somehow was not. More accurately, and in contrast to Prum's views, Darwin's advocacy of female choice made him much more an adaptationist than Wallace: Darwin (1871, chapter 8) recognized the fitness-enhancing benefits from choice for females, which Wallace considered at best superfluous, and which Prum denies in the early chapters of this book.

What matters in resolving scientific controversies are the results of empirical tests of competing hypotheses. Prum claims that in '... nearly 150 years after *The Descent of Man* and 25 years after Grafen's, 1990 paper, there are still no generally accepted, textbook examples of arbitrary mate choice. Period.' (page 72). This claim is contradicted a few pages later where he states: "... a recent 'meta-analysis' ... *did* find significant evidence in support of arbitrary Fisherian mate choice while *failing* to find support for the idea that males who are preferred provide any good genes." (page 76).

The study Prum refers to (Prokop, Michalczyk, Drobnik, Herdegen, & Radwan, 2012) found heritability of male display trait expression and physiological and life history traits, with heritability of male display traits having a stronger effect. However, these results offer less support for LK runaway selection than Prum suggests. Heritability of male display traits is consistent with both good genes and runaway selection, while physiological and life history traits are more consistent with good genes hypotheses. Prokop et al. presented no evidence that male display traits evolved because of arbitrary preferences. Prum does not consider a more recent meta-analysis (Greenfield, Alem, Limousin, & Bailey, 2014), which is more relevant because it tests a key prediction of the LK runaway model. Greenfield et al. found no evidence of genetic correlations between male display traits and female mating preferences.

Prum discusses his reaction to reviewers of an earlier manuscript, who (correctly) indicated that, without evidence, he could not conclude that male pointing behaviour in the courtship display of the golden-winged manakin was caused by runaway selection. Prum claims that this argument is unfair because the runaway selection hypothesis is untestable. He then argues that untestability is a sufficient criterion for him to designate the LK runaway model as the 'null model of sexual selection', which should be considered supported if a test of an alternative hypothesis is rejected. However, this argument violates the fundamental notion of fairness in evaluating hypotheses. Typically, the null is represented by the placebo, that is, the result expected if there is no underlying mechanism, with a strong bias against the alternative/tested hypothesis that is designed to limit false positives. Prum's null model approach reverses this bias by favouring with false positives the 'untestable' LK runaway hypothesis. These tests are based on the performance of other models and with no direct evidence that the LK runaway model actually works. There are many other sexual selection hypotheses, including some that are well supported, suggesting that this null model approach is both logically flawed and unnecessary.

Prum is clearly bothered by the consensus view that beauty in sexual display can be explained as an indicator of health and high performance to prospective mates. As Fisher (1915, page 185) wrote: 'Why have the females this taste? Consider, as an example, two obvious human traits, red cheeks and strong-smelling breath. The one is generally associated with bodily health and vigor, the other with bad digestion, ulcerated throat, or rotten teeth. It would be an advantage to primitive man, even if from the earliest times he had no aesthetic prepossessions, to find a bright complexion pleasant and attractive to him, and, for the same reason, tainted breath offensive.' Prum does not seriously address this widely accepted view and its supporting data except to deride it.

Instead, Prum offers his 'Beauty Happens' hypothesis, claiming, without support and contrary to Fisher, that aesthetic preferences have no function, and that beautiful traits can evolve only by

runaway selection of arbitrary traits. According to this hypothesis, arbitrary male traits and female preferences run away as described in the LK hypothesis, and they are beautiful because beauty is what females prefer. There is, however, remarkably little discussion of obvious questions that emerge from this proposal. Why are traits that females prefer arbitrary? Why do 'arbitrary' avian display traits often appear beautiful to humans? Why are animal and human mating preferences often associated with health and vigor? What physiological mechanisms cause arbitrary male traits to be perceived as beautiful? And, if such preferences are really arbitrary, why is it common for male display traits to be large, ostentatious, and require a high level of male performance? This consistency in the design of male display traits among diverse, highly polygynous species suggests a convergence that Prum (1997) claims should not occur as a result of the LK runaway model.

Despite disparaging an adaptive view of sexual selection for most of the book, Prum uses the same approach to explain interesting behaviours and other adaptations in waterfowl, bowerbirds, manakins and humans. He cites Borgia's (1995) hypothesis that bowerbird bowers evolved as a result of female preferences for males who reduce the threat of sexual coercion. According to this threat reduction hypothesis, (1) females should be careful in approaching males to avoid forced matings, and (2) male behaviours and devices, such as bowers, that reduce threat should be attractive to females as they approach males to assess the quality of their display. Prum relabels this hypothesis 'aesthetic remodeling' and uses it to explain the complex multimale displays of *Chiroxiphia* manakins to visiting females. He maintains that female manakins, like female bowerbirds, avoid sexual coercion, and male manakins that cooperate in display signal a lessened tendency for coercion.

An alternative hypothesis is that manakin males, like bowerbird males, interact in same-sex displays to learn and practice high-performance courtship displays. Females are attracted to pairs of interacting males because the males' ability to attract a social partner and produce highly coordinated complex displays with him reveals his quality as a potential mate. This hypothesis seems more likely than the idea that male–male cooperation leads to less threat to females for two reasons: it better explains the complexity of these manakin displays, and there is no evidence that male–male cooperation lowers the male tendency to sexually coerce females. In fact, in bowerbirds, the age classes most often engaged in same-sex cooperative courtships are also the most aggressive in seeking forced copulations (G. Borgia, personal observation).

In the last chapter of *Beauty*, Prum reveals the political view that has shaped the core arguments in this book. Prum's style and message is a rerun of Gould and Lewontin's divisive writings from 40 years ago, in which they unfairly associated adaptationism with genetic determinism, eugenics and Nazi atrocities (Allen et al., 1975, p. 186). Prum applies similar arguments to sexual selection, associating good genes and adaptive mate choice hypotheses with eugenics and Nazi violence. He states: 'To permanently disconnect evolutionary biology from our eugenic roots, we need to embrace Darwin's *aesthetic* view of life and fully incorporate the possibility of *nonadaptive*, arbitrary aesthetic evolution by sexual selection. ... Accordingly, evolutionary biology should adopt the nonadaptive, Beauty Happens null model of the evolution of mating preferences and display traits by sexual selection' (page 331).

Prum's conflation of eugenics and genocide with adaptive mate choice is a disservice to his readers and colleagues for several reasons. First, this argument is wrong. Mate choice represents individual, and especially female, reproductive freedom, whereas eugenics and genocide represent a restriction by the state on an individual's ability to live and reproduce. It is not more moral to choose a mate

for arbitrary reasons, as Prum suggests, than to choose one to enhance the success of one's offspring. Consistently across societies, parents support the interests of their offspring, suggesting that adaptive mate choice may be viewed as morally superior. Second, Prum's mistaken association of eugenics with adaptive/good genes mate choice represents a threat that can limit free scientific discussion of important issues, and this should be resisted. Third, science validates or rejects hypotheses based on evidence, not on potential or contrived historical associations, altruistic intent, or political belief.

We offer two key takeaways from this book. First, contrary to Prum's claims, LK runaway selection has enjoyed a privileged position, including being prominently presented in evolution and behaviour textbooks despite a lack of supporting evidence. Perhaps the most significant implication of *Beauty* comes from Prum's inability to make a credible case for LK runaway sexual selection in this book's 448 pages, suggesting that it may be time to shift focus to other, better-supported models. Second, Prum's (and other, earlier) efforts to inject politics into science commonly distort the science to justify political goals. We should have all learned by now that science is about understanding what nature is, not what we want it to be. The arguments in *Beauty* that suggest otherwise should be rejected.

Gerald Borgia\*

Department of Biology, University of Maryland, College Park, MD 20742, U.S.A.

Gregory F. Ball

Department of Biology and Psychology, University of Maryland, College Park, MD 20742, U.S.A.  
E-mail address: gball@umd.edu.

\* Correspondence: G. Borgia, Department of Biology, University of Maryland, College Park, MD 20742, U.S.A.  
E-mail address: borgia@umd.edu (G. Borgia).

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