Mate Choice and Null Models

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Biologists have proposed a variety of explanations for extravagant sexual displays, and controversies over explanations define the history of sexual selection research. Recently, Richard Prum has defended Darwin's idea that the evolution of sexual displays is driven by arbitrary and nonadaptive preferences of potential mates. Prum argues that this explanation should be the null model for sexual selection research. I show that if we adopted Prum's proposal, the inferences we could be justified in making are more modest than he claims. I also discuss problems with estimating model parameters that at present prevent his proposal from being useful in practice.

1. Introduction. The club-winged manakin is unique among birds. The males of this South American species have specially shaped feathers and wing bones that they vibrate—faster than a hummingbird can flap—to create a violin-like courtship song. Remarkably, the wing bones that produce the song are solid. In all other flying birds, these bones are hollow, part of the finely tuned morphology that allows birds to fly. Yet club-winged manakins have made a costly departure from this otherwise universal design in order to sing with their wings rather than their throats (Bostwick, Riccio, and Humphries 2012). Why?

This puzzle goes well beyond manakins. Species across the tree of life have evolved costly sexual displays, from elaborate courtship dances to intricate color patterns. They have also evolved preferences for mates with these displays. Accounting for such extravagance is part of the explanatory agenda of evolutionary biology.

Biologists have proposed many explanations for extravagant sexual displays, and controversies about the merits of these different explanations

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†I am grateful to Jonathan Birch, Tom Rowe, and an anonymous referee for their insightful comments on draft versions of this article.

Philosophy of Science, 87 (December 2020) pp. 1096–1106. 0031-8248/2020/8705-0027$10.00
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https://doi.org/10.1086/710614 Published online by Cambridge University Press

define the history of sexual selection research. Most recently, the ornithologist Richard Prum (2010, 2017) has offered a fresh defense of Darwin's idea that the evolution of sexual displays is driven by the arbitrary and often nonadaptive preferences of potential mates. Most biologists start from the assumption that sexual displays typically evolve to signify that their bearers will be hardy, helpful mates or that they will pass on good genes to offspring. But Prum argues that the default hypothesis, or null model, in sexual selection research should be the opposite. Biologists should only invoke adaptive explanations for the evolution of sexual displays when explanations in terms of arbitrary preferences fail. Otherwise, they should accept explanations in terms of arbitrary preferences.

Prum's proposal has been influential. His 2017 book was a Pulitzer finalist, *New York Times* Top 10 Book of the Year, and popular success. It has also been heavily cited and critically reviewed by experts. In this article, I show that arbitrary preference explanations are not yet able to serve as a null model for sexual selection research, although perhaps someday they will be able to. I also show that the inferences researchers could be justified in making as a result of adopting Prum's methodological suggestion are much more modest than he claims. Even if biologists did use arbitrary preference explanations as a null model for testing adaptive explanations for sexual displays, they would still need independent evidence in favor of arbitrary preference explanations before accepting them.

In making these points, I provide two contributions to the literature on null modeling. First, I use accounts of null modeling and statistical hypothesis testing developed by William Bausman, Marta Halina, Peter Godfrey-Smith, and other philosophers to identify and critique a mistaken idea about scientific inference that appears not only in Prum's work but also in arguments made by his critics. Second, I extend these accounts to show that the criteria for determining the suitability of a null model for testing some hypothesis are not entirely formal. A null model's suitability also depends on facts about how model parameters are estimated.

2. Competing Explanations Reviewed. Unlike many other traits, such as alarm calls or acute senses of smell, sexual displays do not evolve because they make it easier to survive in a dangerous world. Nor do they increase the absolute number of offspring organisms can possibly produce. Instead, they evolve either because they improve an organism's ability to compete with members of the same sex (e.g., deer antlers) or in response to the preferences of potential mates. The latter is my focus in this article.

As long as potential mates prefer extravagant sexual displays, it is easy to explain why displays themselves evolve. The real puzzle, then, is how preferences for costly displays that not obviously relevant to survival or fecundity can evolve. The solutions that biologists have provided to this puzzle

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fall into two categories: direct sexual selection and indirect sexual selection (reviewed in Andersson 1994). In direct sexual selection, mate choice preferences increase the fitness of the organism who has them. In indirect sexual selection, mate choice preferences increase the fitness of that organism's offspring.

In some mechanisms of direct sexual selection, the preferences that evolve are arbitrary. That is, the mating preferences are for display traits that themselves are under selection only because they correspond to a mating preference. An example is sensory bias, when mate choice preferences in one sex are under natural selection for a reason unrelated to mate choice. Female guppies may, for example, prefer orange things because that preference helps them find food. This preference may lead them to prefer mates with bright orange spots, but only as a by-product of their sensory bias toward orange things (Rodd et al. 2002).

Other mechanisms of direct selection are not arbitrary. Sometimes, a mating preference is selected because it is for some display trait that correlates with a direct fitness benefit. These direct fitness benefits include food, protection, and parental care. Some biologists believe male cardinals' bright red plumage signals the quality of parental care a father will provide (Linville, Jennions, and Brooks 1998). Indirect sexual selection can also be arbitrary or nonarbitrary. The arbitrary preference mechanism assumes some variation in preferences and some variation in display traits. Members of the sex with preferences choose mates whose displays match their preferences. This assortative mating produces an association between the genes underpinning particular preferences and the genes underpinning the corresponding displays. This association means that not only are the display genes under selection (because one sex prefers the display trait) but also the associated preference genes are now under indirect selection—they hitchhike along with the display genes.

Selection for display trait genes increases selection for preference trait genes, initiating a positive feedback loop that can push trait values for both preference and display to extreme levels. Eventually, these displays can become too costly, and natural selection pushes back against sexual selection, halting the "runaway" evolution of preference and display. This mechanism is sometimes called the Fisher process. It is also called the sexy sons hypothesis, because when females choose sexy mates, it increases the chance that their own sons will be sexy and able to attract mates. But I will use Prum's term, arbitrary preference. The key feature of this mechanism is that both display traits and preference are untethered from anything fitness relevant other than sheer attractiveness. And attractiveness in this case is not about anything. The beautiful is not beautiful because it is good.

An example of a nonarbitrary mechanism of indirect sexual selection is the good genes mechanism. This mechanism works just like the arbitrary

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preference mechanism, with the addition of an initial covariance between the genes underpinning the sexual display and some genes underpinning viability. Viability is naturally selected fitness leftover after excluding fitness due to mate quality or number (Kokko, Jennions, and Brooks 2006, 49). It is fitness due, for example, to intrinsic fecundity or longevity. It is not fitness due to sexiness. The existence of a covariance between viability genes and display trait genes means that when organisms choose attractive mates, they are also choosing ones who have better genes. An example of this mechanism is collared flycatchers, a species in which the size of males' white wing patches is related to body condition, which is an element of viability (Török, Hegyi, and Garamszegi 2003).

The arbitrary preference and good genes mechanisms are similar enough that it is difficult to determine which is the right explanation for the evolution of any particular display-preference pair. The difficulty of distinguishing between the two mechanisms has generated controversy over how common each of them is. Historically, biologists have favored the nonarbitrary mechanisms (direct benefits and good genes), possibly due to an adaptationist bias. The default assumption in much sexual selection research has been that display traits signal either a mate's viability or ability to provide direct fitness benefits.

Prum's proposal inverts this asymmetry. He argues that the arbitrary preference mechanism should be the null model for the other mechanisms I have described. What does it mean to treat the arbitrary preference mechanism as a null model, and why does Prum advocate for this methodological shift?

3. Arbitrary Preference as Null Model. Prum thinks null models have three primary characteristics. First, they are models that build in minimal assumptions (Prum 2010, 3088–89). They try to represent the world as researchers think it is when "nothing special" is going on (Prum 2017, 69). When investigating the evolution of sexual displays and preferences, this means a model can include genetic variation for displays and preferences, because such must exist in order for evolution to occur. But it does not include further evolutionary forces, such as natural selection on display traits.

Second, null models are identical to other models but with some critical parameters set to 0 (Prum 2010, 3098). This feature makes them useful for testing other models. If we can explain some phenomenon using a null model, it casts doubt on the idea that a more complex model is a better explanation. If a null model is insufficient to explain the phenomenon under investigation, this supports the idea that another model is required.

Third, null models cannot be confirmed, only falsified (Prum 2010, 3096; 2017, 71). Null models are not tested directly. Instead, they are tools for testing other models. Rejecting a null model supports some alternative model, but

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failure to reject a null does not confirm it; it just means the null model cannot be ruled out.

Prum justifies his claim that the arbitrary preference mechanism should be treated as a null model in sexual selection research, by appealing to the way null models are used in ecology and molecular evolution (2017, 75). Ecologists use null models to test hypotheses about what causes patterns of species abundance in an ecosystem. They want to know whether patterns of species abundance are caused by interspecific competition. They test this hypothesis by comparing data about species abundance to a null model. The null model predicts how patterns of species abundance would look in the absence of interspecific competition. If the data are similar to the null model's predictions, ecologists consider it a reason not to attribute actual patterns of abundance to competition. But if the data and the model predictions diverge, this supports the idea that competition determines patterns of species abundance.

Null models are used in a similar way in molecular evolution research, in which researchers investigate changes in gene frequencies over time. To test the hypothesis that natural selection drives changes in gene frequencies, they use null models in which gene frequencies are only allowed to change as a result of stochastic processes. If the null model predicts gene frequency patterns that closely resemble actual patterns, this tells against the idea that natural selection is responsible for these patterns. If the null model predicts patterns of change in gene frequencies that diverge from actual patterns of change, researchers take this as a reason to think that natural selection is indeed responsible for these patterns.

In both ecology and molecular evolution, the introduction of null models has been controversial but fruitful. Null models provide a way to test assumptions that were previously taken for granted. In light of this, Prum argues that sexual selection research needs to adopt a null model as well and that because the arbitrary preference mechanism is a simplified version of other sexual selection mechanisms, it is the appropriate null model for testing hypotheses about these explanations.

But Prum's view is not merely that sexual selection research should adopt the arbitrary preference mechanism as a null model. He further claims that until they can reject the null model, researchers should accept the arbitrary preference mechanism as the best explanation for the evolution of display traits and preferences (Prum 2010, 3096). In support of this claim, he argues that it is possible for the arbitrary preference mechanism to occur in nature but impossible to confirm particular instances of it. Demanding confirmation is, therefore, unreasonable (Prum 2017, 71–72). He also says the arbitrary preference mechanism represents biologists' best guess about what is going on in nature in the absence of additional evolutionary forces: "It describes how evolution by mate choice works when nothing special is

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happening—that is, when mates are choosing what they prefer, period" (71). In light of these considerations, researchers should not seek to offer proof for the arbitrary preference mechanism. They should only seek to reject it. When they cannot reject it, they should accept it.

Prum is wrong that the arbitrary preference mechanism should enjoy such privilege. In the next two sections, I show that adopting the arbitrary preference mechanism as a null model does not justify accepting the arbitrary choice mechanism as the best explanation for some data. I also show that researchers can and should try to provide evidence for the arbitrary choice mechanism.

4. Statistical Hypothesis Testing versus Null Modeling. Bausman and Halina (2018) have recently clarified important differences between (*a*) statistical hypothesis testing and (*b*) null modeling, differences that illustrate why Prum is wrong to say researchers should accept the arbitrary preference mechanism whenever they cannot reject it. Theirs is not the only way of justifying statistical hypothesis testing, however (for a review of other approaches, see Godfrey-Smith [1994]). In statistical hypothesis testing, researchers consider variables, perhaps exercise and weight loss, and ask whether there is a relationship between them. The hypothesis that there is a relationship between the variables is called the alternative hypothesis. The hypothesis that there is no relationship between the variables is called the null hypothesis. The null hypothesis functions much like Prum believes null models should function in biology. It gets epistemic privilege.

Researchers consider both hypotheses in relation to some data (e.g., the body weights of exercisers vs. nonexercisers) and calculate how likely these data are, both in a world where the alternative hypothesis is true and in a world where the null hypothesis is true. If it turns out that the data would be very improbable in a world where the null hypothesis is true, researchers reject the null and infer that the data are evidence in favor of the alternative hypothesis. Crucially, it is far more difficult to reject the null hypothesis than it is to reject the alternative hypothesis. In this way, statistical hypothesis testing is biased toward the null hypothesis.

This bias is justified because statistical hypothesis testing is used in experimental and observational contexts where researchers control for extraneous variables (e.g., eating habits) that they know affect the dependent variable(s) that are the focus of the study (body weight, in our example). In these contexts, the null hypothesis that there is no relationship between the focal variables is equivalent to the hypothesis that the influence of extraneous variables explains the experimental or observational data. Researchers' knowledge of the magnitude of the effects of these variables is what justifies their privileging of the null hypothesis over the alternative hypothesis. When they retain the null hypothesis rather than rejecting it, they do not really learn

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anything new. They merely "fail to rule out the possibility that the observed results were caused by those variables the researchers did their best to eliminate" (Bausman and Halina 2018, 30).

Null modeling resembles statistical hypothesis testing in some ways, but the two techniques are different, and they license different inferences. In null modeling, researchers start with a pattern in the world that they want to explain and some original hypothesis that may explain the pattern. They model the hypothesis and compare the output of this "original model" with experimental or observational data (Bausman 2018). Unfortunately, a match between the data and model output cannot confirm the original hypothesis because some other hypothesis researchers have not considered might also match the data. Null modeling is a tool for dealing with this problem. It tests the possibility that patterns researchers desire to explain could be produced without the focal mechanism(s) of the original hypothesis.

The strategy of null modeling is to create a model that leaves out the focal mechanisms of the original hypothesis. Then, researchers compare output from the null model to their data. If the match between data and the null model's output is poor, this is evidence that the original hypothesis produces the pattern of interest. If the match between data and the null model's output is good, this is evidence that the original hypothesis does not produce the pattern of interest.

But null modeling provides no support for the idea that the processes modeled in the null are responsible for producing the pattern of interest. Unlike the null hypothesis in statistical hypothesis testing, a null model is not a model of processes that researchers already know are relevant to producing the pattern of interest. This difference is why privileging the null in statistical hypothesis testing is justified, while privileging the null in null modeling is not.

5. Null Model, Not Null Hypothesis. Prum claims that researchers should accept the arbitrary preference mechanism as the best explanation of the data whenever they fail to reject the null. For this to be correct, the arbitrary preference mechanism would have to function like the null hypothesis in statistical hypothesis testing. But it does not. Consider the quantitative genetic model of the arbitrary preference mechanism from Fuller, Houle, and Travis (2005) that is Prum's (2010) preferred null model.

The Fuller et al. model includes the following variables: *sexual selection* on display traits, *variation* in genes underpinning mating preferences and display traits, and *covariances* between genes underpinning mating preferences and display traits. The model represents the effects of these variables on the dependent variables of interest: mating preferences and display traits. In Prum's view, selection, variation, and covariances are extraneous variables already known to influence the dependent variables of interest. In a

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sense, this is correct. Researchers know that selection, variation, and covariances affect mating preferences and display traits. After all, these variables affect mating preference and display trait values in models of any of the sexual selection mechanisms described in section 2. So, this model of the arbitrary preference mechanism is equivalent to models of other sexual selection mechanisms, but with some parameter values set to 0.

To treat this model of the arbitrary choice mechanism as a statistical null, however, researchers would have to know, not just that selection, variation, and covariances affect mating preferences and display traits but also the magnitudes of their effects. This knowledge is necessary for calculating how likely it is that these variables alone could account for actual mating preference and display trait values. But researchers do not know the magnitude of the effects of these variables in any particular experimental or observational context. In statistical hypothesis testing, researchers design experiments with treatment and control conditions so they can quantify the effects of the extraneous variables referenced in the null hypothesis, but there is no analogous method for quantifying the effects of the relevant variables of the arbitrary preference mechanism.

This means researchers should not accept the arbitrary preference mechanism whenever they fail to reject it. If researchers adopted the Fuller et al. model as a null, it could only provide evidence for or against other mechanisms of sexual selection (e.g., the good genes mechanism).

If researchers cannot prove a null but also should not accept a null simply because they fail to reject it, where does this leave the issue of arbitrary preferences versus good genes? The answer is simple. The claim that we cannot prove a null only holds within the confines of null modeling, and the arbitrary preference mechanism's status as a null model is context dependent. There is nothing about using a null model in one context that prevents researchers from investigating the hypothesis underling the null in another context. Determining what data would count as evidence for the arbitrary preference mechanism is of course difficult but not impossible.

So, the arbitrary preference mechanism is not a statistical null hypothesis. The final issue to consider is whether it is a suitable null model for sexual selection research. Several critical reviews of Prum's book have argued that the arbitrary preference mechanism is not a suitable null model. But in each case, the authors argue in a way that indicates confusion about the distinction between statistical hypothesis testing and null modeling.

Patricelli, Hebets, and Mendelson (2019), for example, write that the arbitrary preference mechanism cannot be a suitable null model because it "contains many testable causal relationships" (118). Recall that a null hypothesis (in the statistical hypothesis testing sense) is equivalent to the hypothesis that there is no relationship between the focal variables in the alternative hypothesis. Since the focal variables of the arbitrary preference

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mechanism are also focal variables for the good genes mechanism, Patricelli et al. dismiss the possibility that the arbitrary preference mechanism could be a good null model for the good genes mechanism. There are two mistakes here. First, the arbitrary preference mechanism is null with respect to the relevant causal relationship—selection on viability due to a covariance between genes underpinning viability and genes underpinning a display trait. More importantly, the fact that the arbitrary preference mechanism is not a suitable null hypothesis does not mean it is not a suitable null model. Although not recognized in the sexual selection literature, the two issues are independent.

One reason to think the arbitrary preference mechanism is a suitable null model, at least for the good genes mechanism, is that it excludes the focal causal process of the good genes mechanism: natural selection on viability when viability is correlated with sexual displays and mating preferences. But excluding the focal causal process of the original model is not the only criterion a suitable null model must meet.

A suitable null model should meet at least one further criterion. It should make different predictions than the original model does. The essence of the null modeling strategy is to compare the null's predictions to some experimental or observational data. Such a comparison is pointless if the null and original models make identical predictions. It would be trivial that the null model is sufficient to produce whatever pattern researchers are interested in explaining.

Successful uses of null modeling in other areas illustrate this point. The null models ecologists use to test the hypothesis that species abundance is determined by competition among species exclude interspecific competition. The patterns of species abundance these null models predict are not identical to the patterns of species abundance predicted by models that include interspecific competition. The same is true in molecular evolution research. Models that allow gene frequencies to change only as a result of stochastic processes and models that allow gene frequencies to change as a result of natural selection do not yield identical predictions. If they did, the null models would not meaningfully test the hypothesis that changes in gene frequencies are driven by natural selection.

The Fuller et al. (2005) model of the arbitrary preference mechanism does not meet this second criterion, at least not at present. To see why, contrast their model of the arbitrary preference mechanism with their model of the good genes mechanism. These two models need to make different predictions about the values of mating preferences and display traits. An important independent variable in the good genes model is viability (naturally selected fitness leftover after excluding fitness due to mate quality or number). To predict values for mating preferences and display traits, the good genes model must quantify the viability of organisms who possess display traits.

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Viability estimates are beset with problems (Kokko et al. 2006). Viability cannot be measured directly, so biologists often use another fitness component, perhaps longevity, as a proxy. But life history theory casts doubt on this practice. No organism, not even a highly viable one, can maximize every component of fitness (longevity, growth rate, immunocompetence, etc.). So, life history theory predicts trade-offs. Optimal trade-offs differ across environments, so there is no reason to expect any single fitness component always to be positively related to viability and therefore a reliable proxy for it.

One solution to this problem is to use total fitness (as expressed by an organism's breeding value) as a proxy for viability. But this solution combines fitness due to viability with fitness due to sexiness, which is precisely what needs to be kept separate in order to test the good genes mechanism. If viability estimates in good genes models include fitness due to sexiness, then the predictions of the arbitrary choice null model will not differ from the predictions of the model of the good genes mechanism.

A further problem is that highly viable organisms can allocate resources to maximizing attractiveness at the expense of other fitness components (Kokko 2001; Kokko et al. 2002). In practice, then, display trait values under the arbitrary preference scenario might be identical to display trait values under the good genes scenario. If so, the patterns predicted by the two models will be indistinguishable. The null model will not distinguish between cases in which the null is and is not sufficient to produce the pattern of interest.

These problems may have solutions. Conceptually, the arbitrary preference mechanism is a suitable null model for other mechanisms of sexual selection, because it does exclude causal processes that are central to these other mechanisms. Practically, the model Prum proposes as a null does not allow researchers to learn anything new by comparing the output of the null model to their data. Perhaps these practical problems are not permanent. There may be creative ways of estimating viability that better manage the fact that organisms flexibly allocate resources to maximizing different components of fitness. Although there are challenges for his proposal, Prum may be right that sexual selection research needs a null model and that the arbitrary preference mechanism is the best choice.

6. Suitable Null Models. Philosophical analysis of null modeling has focused primarily on the inferential strategy behind null modeling. Discussion of what makes something a suitable null model has been limited to the idea that a null model must exclude the focal causal mechanism of the original hypothesis. But the case I have analyzed in this article makes it clear that we cannot judge a null model's suitability merely by examining its form. A null model's suitability also depends on facts about how model parameters are estimated, and its suitability may change over time as scientists' ability to estimate parameter values improves. In this way the inferential strategy

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behind null modeling is like many other types of scientific inference: the difference between a good and bad inference cannot be captured by differences in form alone, because strategies for gathering evidence (e.g., for sampling and parameter estimation) also matter (Godfrey-Smith 2003).

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