THE LANDE–KIRKPATRICK MECHANISM IS THE NULL MODEL OF EVOLUTION BY INTERSEXUAL SELECTION: IMPLICATIONS FOR MEANING, HONESTY, AND DESIGN IN INTERSEXUAL SIGNALS

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The Fisher-inspired, arbitrary intersexual selection models of Lande (1981) and Kirkpatrick (1982), including both stable and unstable equilibrium conditions, provide the appropriate null model for the evolution of traits and preferences by intersexual selection. Like the Hardy–Weinberg equilibrium, the Lande–Kirkpatrick (LK) mechanism arises as an intrinsic consequence of genetic variation in trait and preference in the absence of other evolutionary forces. The LK mechanism is equivalent to other intersexual selection mechanisms in the absence of additional selection on preference and with additional trait-viability and preference-viability correlations equal to zero. The LK null model predicts the evolution of arbitrary display traits that are neither honest nor dishonest, indicate nothing other than mating availability, and lack any meaning or design other than their potential to correspond to mating preferences. The current standard for demonstrating an arbitrary trait is impossible to meet because it requires proof of the null hypothesis. The LK null model makes distinct predictions about the evolvability of traits and preferences. Examples of recent intersexual selection research document the confirmationist pitfalls of lacking a null model. Incorporation of the LK null into intersexual selection will contribute to serious examination of the extent to which natural selection on preferences shapes signals.

KEY WORDS: Arbitrary traits, Fisher process, honest indicators, intersexual selection, null model, sensory bias.

The popularity of intersexual selection theory has produced a diversity of models of trait and preference evolution, repeated attempts at theoretical unification, and multiple suggestions about how to test intersexual selection mechanisms more effectively (for recent reviews of sexual selection mechanisms, see Rice 2004; Fuller et al. 2005; Kokko et al. 2006). Amidst the diversity of theoretical viewpoints, however, a few nearly universally held opinions guide most current empirical research. First, various mechanisms of intersexual selection are considered to be alter-native hypotheses or variations within a continuum. There is no generally acknowledged null model of evolution by intersexual selection. Second, mating preferences are generally assumed to be under selection for the evolution of display traits that will indicate a male's better genes, better condition, better parental investment, or provide a female with greater mate choice efficiency, etc. Secondary sexual display traits are frequently assumed to be correlated with male quality or condition (i.e., signal information), to provide additional direct benefits during mate searching

(i.e., signal design), or an optimal balance of both. Consequently, the goal of much empirical work in intersexual selection is to confirm the origin of the signal honesty and sensory efficiency rather than to test its existence.

A fundamental problem with the current theoretical and empirical literature on intersexual selection is the absence of a functioning null model. By assuming selection on mating preference in addition to the indirect benefit of the genetic correlation between mating preference and display traits (which I will refer to as natural selection) and additional correlations between viability and traits and preferences, many research programs exist merely to confirm these effects. In confirmationist research, negative results are interpreted as failure to have yet looked hard enough to find the evidence of additional selection on preferences. In this regard, the field of intersexual selection is similar to the state of evolutionary genetics prior to the development of the neutral theory (Nei 2005), and community ecology before the development and adoption of null and neutral models (Gotelli and Graves 1996; Hubbell 2001). Population genetics was dominated by a selectionist paradigm that assumed genetic variation was maintained by natural selection, and neutral genetic variation was not considered to exist. The field was permanently altered by the proposal of the neutral theory by Kimura and Crow (1964) and others (Nei 2005). Likewise, community ecology was dominated by the MacArthurian paradigm that proposed that competition structures communities (MacArthur 1972), until Hubbell (1979), Strong (1980), and others showed that some ecological patterns that had been attributed to competition were entirely consistent with stochastic processes. Subsequently, null models have become fundamental to community ecology and brought great benefits of the field (Gotelli and Graves 1996; Hubbell 2001).

Intersexual selection is in need of a null model revolution. The a priori assumption of natural selection on mating preferences has created a distorted view of reality in which the null mechanism does not even exist. Much of intersexual selection research is an extant remnant of the "adaptationist programme" (Gould and Lewontin 1979) in which the deterministic power of natural selection is assumed and alternative explanations are defined out of existence or treated as irrelevant. Here, I propose that the broadly Fisherian (Fisher 1915, 1930, 1958) sexual selection models of Lande (1981) and Kirkpatrick (1982), including both stable and unstable equilibrium conditions, provide the appropriate null model for the study of the evolution of intersexual traits and preferences. I discuss the role of null models in evolutionary biology and intersexual selection. I review the different predictions made about the evolution of trait meaning, honesty, and design through various intersexual selection mechanisms. I discuss the common view that Fisherian and Lande–Kirkpatrick (LK) models have little relevance to nature, and review the predicted differences in trait-preference evolvability between the LK null

and other intersexual mechanisms. I then present recent examples of the intellectual pitfalls of confirmationist sexual selection research in the absence of a null model. The examples come from avian biology that has been the subject of extensive intersexual selection research. By using a diversity examples of from a single clade, I hope to document the compound detrimental effect of absence of a null model on our understanding of the evolution of the secondary sexual display traits of an entire group of organisms.

Lande–Kirkpatrick as the Null

Kirkpatrick (1987) and Kirkpatrick and Ryan (1991) proposed an explicit null model of intersexual selection as a pedagogical tool unifying the mathematical models of various intersexual selection mechanisms. Given genetic variation for a display trait and a mating preference, the most sexually advantageous trait value for any male to possess is the one that matches the mean female preference (Fig. 1A). In the presence of natural selection on the display trait, intersexual selection and natural selection acting on the display trait should establish a line of population equilibria between the two forces (Fig. 1A). This is the Kirkpatrick and Ryan (1991) null model; however, Kirkpatrick and Ryan chose to present the full dynamics and consequences of their null model in a separate section about the Fisherian "runaway process" without discussing the stable Fisher conditions. The general assumptions of the Kirkpatrick (1987) and Kirkpatrick and Ryan (1991) null models and the Fisher "runaway" process are identical.

The adjective "Fisherian" has been used in so many different and distinct senses that I will not employ it generally here except in reference to previous statements in the literature that refer specifically to features of the proposed null model. Instead, I will refer to the null model as the Lande–Kirkpatrick (LK) mechanism. A quantitative genetic version of the LK null model using the recent framework of Fuller et al. (2005) is presented in the Appendix. Recognizing the LK process as the null model of intersexual evolution merely follows through on the full intellectual implications of the Kirkpatrick and Ryan (1991) framework.

As Fisher (1915, 1930, 1958) proposed and Lande (1981) established explicitly, assortative mating between individuals with extreme display traits and mating preferences will establish a genetic correlation between trait and preference. When a trait and preference are genetically correlated, selection on the trait by the preference can also select for change in the preference itself. The strength of genetic correlation and the amount of genetic variation for the trait will establish the evolutionary trajectory of a nonequilibrium population (Lande 1981). Going well beyond Fisher's verbal model, Lande (1981) and Kirkpatrick (1982) discovered that if the genetic correlation is weak relative to genetic variation for the trait, then nonequilibrium populations will
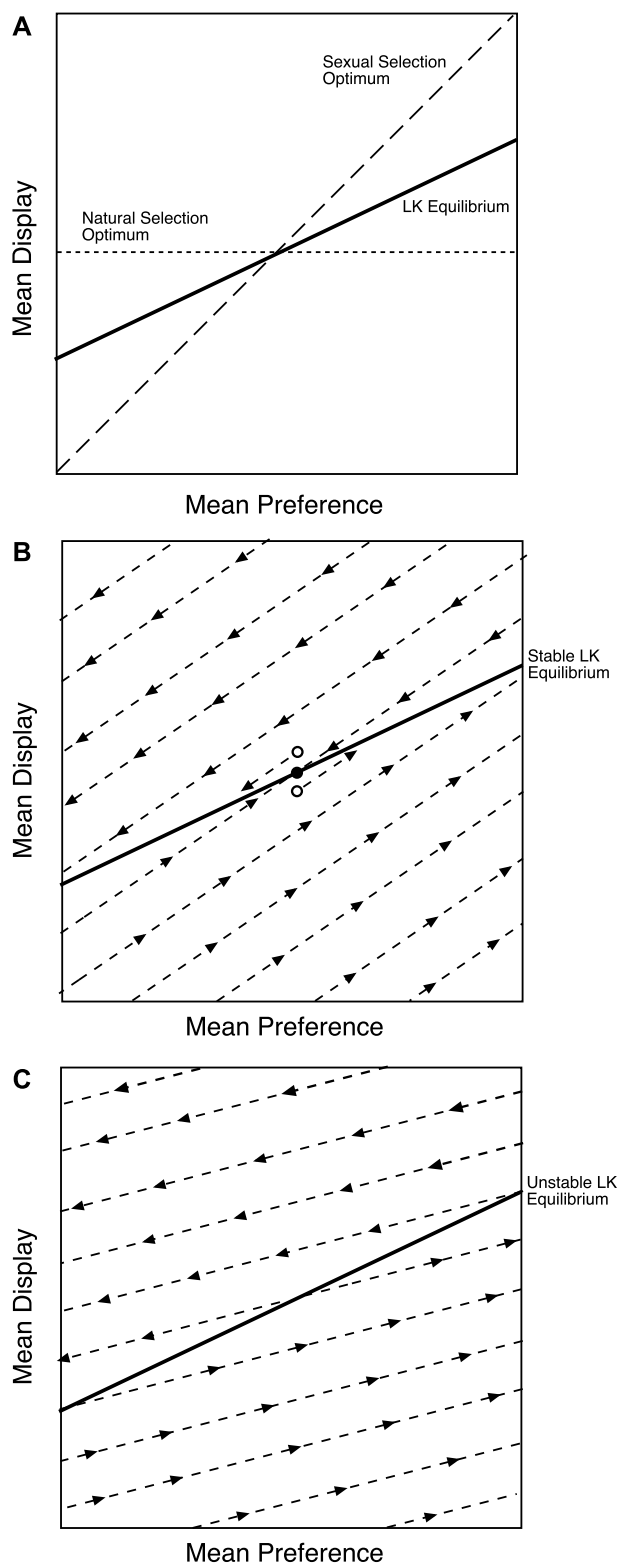
converge on a stable equilibrium line (Fig. 1B). (Although the existence of a stable equilibrium is a direct consequence of the Fisherian conditions, Fisher clearly did not anticipate or predict its existence—another reason to attribute the null model to Lande and Kirkpatrick, rather than to Fisher.) If the genetic correlation is great relative to genetic variation for the trait, then the line of equilibrium will become unstable and populations will evolve exponentially away from the line of equilibria (Fig. 1C, Lande 1981). This latter condition in the LK quantitative description of Fisher's runaway process. Theoretically a runaway will continue until changes in the assumptions arise (Lande 1981). Whether the LK equilibrium will be stable or unstable conditions depends upon the relative genetic variance of trait and preference, and indirectly on the nature of mutation pressure on each (Appendix). Further, dominance or epistasis for genes affecting the trait will create a weaker but deterministic force that can move populations along the line of equilibrium (Gomulkiewicz and Hastings 1990; Otto 1991).

As Lande (1981) and Kirkpatrick (1982) document, the general assumptions of Fisher's verbal model—genetic variation in trait and preference in the absence of natural selection on preferences and additional viability correlations—create rich evolutionary dynamics in addition to the well-known runaway. For example, substantial evolutionary elaboration of trait and preferences can occur through drift away from a stable equilibrium and the evolution of a population toward a new equilibrium rather than a return to the former state (Fig. 1B, Lande 1981). It is essential to emphasize that the LK mechanism proposed here as the null model of evolution by intersexual selection is not synonymous merely with the quantitative conditions of a Fisherian runaway. The LK process encompasses all of evolutionary consequences of existence of genetic variation for traits and preferences in the absence of additional selection on preferences or correlations with heritable components of viability.

Although natural selection on the display trait is often assumed in the Fisher/LK process, it is neither necessary nor determining. The presence of natural selection on display traits

Figure 1. Evolution of mean display trait and mating preference by the Lande-Kirkpatrick (LK) null model (based on Lande 1981; Kirkpatrick and Ryan 1991). (A) The LK mechanism establishes a line of equilibria (dark line) between the sexual selection optimum display trait (dashed line) and the natural selection optimum trait (dotted line). (B and C) Populations will evolve along trajectories (dotted lines with arrows) determined by the relative magnitude of trait/preference genetic correlation and genetic variation for the trait (Lande 1981). (B) If the line of equilibria is stable, then populations will evolve toward a stable line of equilibrium. If a population at equilibrium (filled circle) drift away from equilibrium (open circles), then small differences in the direction of drift will lead to evolution of very different equilibrial combinations of mean trait and preference. (C) If the line of equilibria is unstable, then populations will evolve toward increasingly extreme combinations of mean trait and preference that is the quantitative description of the Fisher runaway process (Lande 1981).

produces only quantitative changes in the slope of the line of equilibria and the outcome of trait/preference coevolution when disrupted from equilibrium, and not qualitative changes in the evolutionary dynamics of the LK model (Lande 1981; Kirkpatrick 1982; Kirkpatrick and Ryan 1991) (Fig. 1, Appendix). Although it is infrequently discussed, it is easy to imagine display trait variations that might not be under natural selection such as various combinations of equally brilliant colors, or equivalently loud and localizable vocal advertisements, etc.

In summary, Fisher (1915, 1930, 1958) proposed that the existence of genetic variation in display trait and corresponding mating preference have complex, intrinsic evolutionary consequences including the possibility of a runaway. Lande's (1981) quantitative genetic models demonstrated the richness of these consequences in new quantitative detail including the existence of a stable line of equilibrium. Kirkpatrick (1982) demonstrated essentially identical evolutionary dynamics with a haploid genetic model. Together, Lande (1981) and Kirkpatrick (1982) document that the evolutionary dynamics of the LK process are extremely robust to variations in the specific genetic assumptions of the models themselves.

In contrast to the null LK model, most other intersexual selection mechanisms assume: (1) additional selection acting on mating preferences in addition to their genetic correlation with the trait, and (2) positive correlations between heritable genetic components of viability and the trait in addition to the direct effects of the display trait on (male) survival, and (3) positive correlations between viability and mating preference (Fuller et al. 2005; Kokko et al. 2006; Appendix). These mechanisms vary in whether the additional selection on mating preferences and fitness correlation evolve to provide indirect genetic benefits (i.e., good genes), or direct benefits such as better mate condition, parental investment, parasite avoidance, greater mate searching efficiency (i.e., sensory drive), or avoidance of sexual manipulation (e.g., sexual conflict in the narrow sense) (Andersson 1994; Fuller et al. 2005; Kokko et al. 2006).

Traditionally, sexual selection has been defined as the result of variation in the number of mates (Arnold and Wade 1984; Endler 1986; Arnold 1994; Shuster and Wade 2003), and variation in mate quality has been considered a component of natural selection. Consequently, selection for preferences that favor traits associated with direct and indirect fitness benefits in addition to the indirect Fisherian benefit of having sexually attractive offspring are defined as natural selection on preference. Recently, however, several authors have redefined sexual selection as any selection arising as a result of variation in both the number and quality of mates (e.g., Fuller et al. 2005; Kokko et al. 2006). Thus, this framework redefines most additional sources of selection on preferences as sexual selection. Although this can be mathematically convenient, this terminology obfuscates fundamental qualitative

differences in the nature and the outcomes of different sources of selection on mating preferences. To clarify the distinction between the null and the adaptive models of intersexual selection, I will adopt the more traditional approach defining sexual selection more narrowly (Arnold and Wade 1984; Endler 1986; Arnold 1994; Shuster and Wade 2003). However, the model presented in the Appendix follows the models of Fuller et al. (2005) and Kokko et al. (2006).

Merely as a consequence of their phenotypic expression, mating preferences create direct sexual selection on display traits and indirect sexual selection on themselves through their genetic correlation with display traits alone. This source of selection on preference is intrinsic because it arises purely as a consequence of the existence of genetic variation in trait and preference. In contrast, all other sources of selection acting on mating preferences arise through the correlations of either trait or preference values with variation in other extrinsic factors—including genetic quality, condition, disease history, parasite infection, capacity for parental investment, migration arrival date, sensory environment, mate choice efficiency, etc. In the case of sensory bias, natural selection on preferences arises through a correlation with some other pleiotropic function of the neural systems that is extrinsic to mate choice. In narrow-sense sexual conflict models, natural selection on preferences arises through the correlation of preference with direct costs of female mating rate (Fuller et al. 2005; Kokko et al. 2006). All of these sources of selection arise through correlations of trait or preference with variation in other extrinsic factors. Because all these additional sources of selection on mating preferences lead explicitly to the prediction of adaptive evolution in preference relative to the variation in these extrinsic factors, I will refer to these additional sources of selection on mating preferences as natural selection. For convenience, I will occasionally refer to models that incorporate natural selection on preferences as adaptive mate choice models. In this framework, sexual selection on preference is an indirect consequence merely of the existence of preference itself, whereas natural selection on preference may be either direct or indirect.

The LK process is the intellectually appropriate null model for intersexual selection because it is the intersexual selection model that makes the minimum assumptions about evolutionary process (Kirkpatrick and Ryan 1991). The LK process assumes genetic variation in both trait and preference. It allows for, but does not require, additional natural selection on the display trait. These elements provide a simple, nontrivial null model of evolution by mate choice.

Like the Hardy–Weinberg equilibrium, the LK model emerges merely from the existence of genetic variation itself in absence of any additional, extrinsic forces, or correlations. Like the Hardy–Weinberg equilibrium (Hardy 1908), the roots of LK model were proposed first proposed by Fisher (1915) in the early

20th century at the dawn of quantitative investigation of evolutionary process when the evolutionary consequences of genetic variation itself were primary research interest. It is also worth noting that R. A. Fisher also coined the term "null hypothesis" (Oxford English Dictionary 2005). Thus, it may not be surprising that the Fisher-inspired LK mechanism would be the appropriate null model for the discipline.

Like the Hardy–Weinberg equilibrium, the LK null model is equivalent to other intersexual selection models with the magnitude of additional variables equal to zero (Fuller et al. 2005; Kokko et al. 2006, Appendix). Hardy–Weinberg equilibrium genotype frequencies will be established immediately in one generation in the absence of any intervening force. Likewise, if there is genetic variation in trait and preference and cessation of other selection on preference, any intersexual selection mechanism will be vulnerable to the immediate establishment of an LK null process. For example, trait mutations that erode the correlation between the preferred trait value and viability will evolve rapidly whenever they arise, and quickly establish an LK process. Thus, the LK model is an appropriate null because it lies at the heart of other intersexual selection mechanisms as a potential intrinsic consequence of genetic variation in trait and preference alone.

Of course, the LK mechanism differs fundamentally from Hardy–Weinberg because of its complex evolutionary dynamics that cannot be described by a single, simple equilibrium. Consequently, the LK mechanism is also a lot more interesting. Unlike Hardy–Weinberg, the LK mechanism will create a line of equilibria that may be stable or unstable (Fig. 1B,C). Populations will evolve to equilibrium along complex trajectories, and drift will foster rapid differentiation among geographic populations (Lande 1981; Kirkpatrick 1982; Kirkpatrick and Ryan 1991). Rejecting the null model in intersexual selection is going to be substantially more difficult than for Hardy–Weinberg.

Few authors have recognized the intellectual contribution of the Kirkpatrick and Ryan (1991) null model (for a rare exception, see Turner and Burrows 1995). Instead, the LK mechanism, and the Fisher runaway process more specifically, have been overwhelmingly viewed as an alternative intersexual selection mechanism, and not as a potential null model. The increasing appreciation of the theoretical continuum among intersexual selection mechanisms—particularly the Fisher process broadly defined and indirect sexual selection for good genes—has led to the proposal that the Fisherian–LK models are not a distinct mechanism but just an extreme in a continuum (Kokko et al. 2002). I will argue that the LK process leads to very distinct predictions about the arbitrary nature of traits (see below). These stark distinctions are exactly why the Fisherian and LK models have elicited such strongly negative responses (e.g., Grafen 1990). As in population genetics and ecology, however, the existence of a unified framework is not reason alone to obfuscate the important distinctions

between the null and alternative models. Furthermore, the recognition of a theoretical continuum has not yet led to the reappraisal of the relevance of the null sexual selection process to nature which I advocate. Rather, it is more likely that features that are intrinsic consequences of the LK null process will come to be seen as attributes of other intersexual selection mechanism in ways that avoid appropriate attribution to null sexual selection process (e.g., trait preference genetic correlation, see Kokko et al. 2002).

The LK mechanism may not be the appropriate null model for all instances of intersexual selection. If there is no genetic variation in either the preference or the trait, or if mating success is determined by proximate stochastic factors (e.g., previous mating success, Alonzo 2008), then the Fisher process is not an appropriate null model. For example, evolution of a novel display trait by a sensory bias mechanism may proceed in the absence of genetic variation in preference. But without coevolution, sexual selection in the absence of genetic variation of either trait or preference will not contribute substantially to evolutionary radiation among populations and species. Thus, in most cases, the LK mechanism remains the appropriate null model of evolution by intersexual selection.

Null Models in Evolutionary Biology

What are the general justifications for null and neutral models in evolutionary biology? Null and neutral models offer simpler or less-deterministic explanations of evolutionary and ecological processes (Nitecki and Hoffman 1987; Gotelli and Graves 1996). Null models are identical to alternative models with values of some critical parameter(s) set to zero (Appendix). Null models explore the contribution of intrinsic mechanisms to determine evolutionary outcomes. Refutation of a null model provides greater support for the alternative model than does mere confirmation of the alternative. In this way, null models are justified by their suitability for hypothesis testing.

Parsimony is often cited as an intellectual advantage of null models. Given that there is no a priori scientific reason to expect the world to be simple, what is the role of parsimony—and null models—in scientific explanation? Elliot Sober (2006a and other references therein) has demonstrated that parsimony is not defensible in the generalized way implied by the notion of Occam's razor. Rather, parsimony has distinct justifications in different scientific contexts—for example, in phylogenetic analysis versus regression. In evolutionary model selection, parsimony can trade-off with complexity, and therefore with model likelihood (i.e., goodness of fit). In other words, complex models can describe variation in data more easily, but increasing model complexity should come with a penalty because inclusion of enough parameters in a model can ultimately be used to engineer a perfect fit with any data. Thus, there must be a balance between model simplicity

and likelihood. In this way, null models can have an advantage over more complex models. In the case of intersexual selection, however, it is not yet clear whether adaptive intersexual selection models actually do provide better fit to the data from the natural world than does the null LK process, or whether the consensus opinion has arisen because researchers have merely tried harder.

In contrast with a hypothesis-testing framework, there are other approaches to quantifying the possible advantage of the parsimony of a null model. A Bayesian approach to hypothesis comparison states that, given a set of observations, the probability of the truth of a hypothesis is the product of the likelihood of the data given that hypotheses and its prior probability. In comparative form

$$P(H_1|O) > P(H_2|O) \quad \text{if and only if} \quad P(O|H_1)P(H_1)$$
$$> P(O|H_2)P(H_2)$$

(Sober 2006a). In Sober's (2006a: 534) words, "If parsimony influences plausibility, it must do so through prior probabilities, likelihoods, or both." In the context of intersexual selection, the essential questions become—What are the likelihoods of the null and alternative mechanisms? What are the prior probabilities of natural selection on mating preferences and the existence additional viability correlations? The majority opinion in the current literature is that the prior probability of natural selection on mating preferences is 1. This perspective is striking reminiscent of the skeptical view of the existence of neutral genetic variation prior to the development of neutral theory. The simplistic assumption of ubiquitous natural selection on mating preferences obfuscates the extraordinary diversity of organismal breeding systems, display behavior, mating behavior, and parental care that create highly variable opportunities for natural selection to act on mating preferences. Adopting the LK mechanism as the null model in intersexual selection will focus research productively on this currently untested assumption.

It is important to note here that the LK mechanism and other mate choice models are not nested models. The condition of adaptive mate choice models—natural selection on mating preferences and viability correlations are nonzero—is specifically excluded from LK models, and vice versa. Like Hardy–Weinberg, the point in parameter space occupied by the LK null model—in which natural selection on preferences, etc. are zero (Appendix)—is not included in the other models. Thus, the Fisherian model has an independent (and thus potentially higher) prior probability, which null models require (Sober 2006a).

The Hardy–Weinberg equilibrium is an example of an uncontroversial null model in evolutionary biology. However, the introduction of null models in evolutionary genetics and community ecology created great controversies (Gotelli and Graves 1996; Nei 2005). In these historic debates, a key criticism of null mod-

els has been that they are nihilistic—that is, implying that nothing matters. But null models actually focus on the extent to which intrinsic forces matter in determining the evolutionary outcomes we observe. As Fisher perceived, the intrinsic consequences of genetic variation in traits and mating preferences themselves should be considered a matter of great importance to study of intersexual selection. It is not nihilistic to state that the evolutionary outcomes of intersexual selection may be determined by the complexity of these intrinsic interactions alone.

Arbitrary Versus Indicator and Efficient Traits

The LK mechanism has many fascinating evolutionary implications for geographic differentiation and speciation (Lande 1981; Kirkpatrick 1982; West-Eberhard 1983), but among the most fundamental implications of the null model concerns the evolution of meaning, honesty, and design of secondary sexual signals. Inherent in Fisher's original proposal is that when genes for a preference select on genes for a trait alone, the evolutionary consequences are arbitrary. This is because the fitness advantages of the trait exist only through its coevolution with preference. Thus, the null LK mechanism predicts that the evolution of arbitrary traits that communicate only an individual's availability and motivation to mate. An arbitrary trait merely corresponds to the preference that has coevolved with it. In this context, the word arbitrary does not mean that the trait is random, ahistorical, accidental, or inexplicable. Rather, arbitrary means that a signal communicates no additional information other than its existence as a display, its availability for evaluation by potential mates, and its potential to correspond to a mating preference. An arbitrary display trait is merely an invitation to intersexual evaluation. An arbitrary trait is neither honest nor dishonest because it does not communicate any information that can be untruthful or falsified. Arbitrary traits do not indicate anything other than availability to mate.

In contrast, natural selection on mating preferences and trait-viability correlations are predicted to result in the evolution of indicator traits whose variation encodes additional information about other properties of the individual who displays the trait, such as genetic quality, physiological condition, disease infection, capacity for parental investment, etc. (Andersson 1994). Alternatively, natural selection on preferences for efficiency in mate searching may select for efficient traits that are less costly to detect and evaluate (Endler and Basolo 1998). The distinction between arbitrary and indicator/efficient traits is fundamental because it concerns the meaning and design of display traits used in intersexual communication (Espmark et al. 2000). Arbitrary traits have no additional meaning beyond their potential to correspond to a mating preference. By contrast, indicator traits are hypothesized

to be a veritable BioMatch.com profile of genomic information, maternal effects, health records, aerobic fitness data, dietary preferences, resource acquisition records, cultural affiliations, and an honest sexual history. In addition to signal meaning, natural selection for mate choice efficiency is hypothesized to lead to the evolution of mating preferences for traits that exhibit efficient design for the detection and transfer of information. Thus, the LK null mechanism predicts that intersexual communication traits are devoid of meaning and design beyond their potential correspondence to preferences, whereas adaptive mate choice mechanisms predict that traits encode volumes of relevant information and are efficiently designed for its transfer.

Kokko et al. (2002) argued that arbitrary traits have not been clearly defined and cannot be distinguished from indicators of viability (good genes). Inexplicably, Kokko et al. fails to consider that arbitrary traits are arbitrary precisely because they do not indicate or correlate with any information, and that good genes or condition indicators evolve precisely because they do. Contra Kokko et al. (2002), the distinction between arbitrary traits and indicator/efficient traits is the most fundamental of all predictions in intersexual selection theory. The recognition of a quantitative continuum between sexual selection models cannot be allowed to obfuscate this issue. Whether intersexual traits exhibit any meaning or design other than their arbitrarily coevolved correspondence with mating preferences should be of primary interest to all researchers in intersexual selection.

Is the Null LK Process Mythical?

The completion and elaboration of Fisher's idea about the intrinsic consequences of genetic mating preferences through the explicit genetic models by Lande (1981) and Kirkpatrick (1982) constituted a major intellectual achievement in evolutionary biology. Yet, starting with Grafen's (1990) statement that "To believe in the Fisher-Lande process as an explanation of sexual selection without abundant proof is methodologically wicked," the Fisher and LK mechanisms have been generally treated as a hypothetical possibility of merely theoretical interest (e.g., Kirkpatrick and Ryan 1991; Fuller et al. 2005). Hauser's (1998) book on the evolution of communication only mentions the Fisher process in a table. Espmark et al.'s (2000) edited volume on animal signals makes no mention of the Fisherian or LK mechanisms at all. In *Evolution of Animal Communication*, Searcy and Nowicki (2005: 80) consider it "an open question whether mating signals that have evolved by the Fisher mechanism exist at all, let alone whether they are common." Furthermore, many authors have used their skepticism about the likelihood of a Fisherian runaway to discredit any consideration of the evolutionary dynamics that arise intrinsically from the existence of trait and preference variation alone.

For example, the "paradox of the lek" was originally proposed by Kirkpatrick and Ryan (1991: 33) in the general form, "Why should females have evolved such strong preferences when they seem to receive no tangible benefits from their choice?" However, the paradox of the lek has been consistently redefined more narrowly by subsequent authors to refer exclusively to the maintenance of adaptive advantages to mate choice through trait condition dependence and genetic variance in condition (e.g., Rowe and Houle 1996; Tomkins et al. 2004; Kotiaho et al. 2007), to the complete exclusion of consideration of the LK null process that provides an entirely consistent resolution of the paradox (Kirkpatrick and Ryan 1991). Natural selection is not required to resolve the paradox of the lek, unless the paradox is redefined to insure it.

The critical view of the Fisher process has been broadly applied to all arbitrary intersexual traits. There is not a single, generally accepted, textbook example of an arbitrary secondary sexual trait in any organism. Jones et al. (1998) reported support for the predictions of the Fisherian process in a lekking sand fly. Prum (1997), Durães et al. (2009) and Price and Whalen (2009) have presented data as consistent with an arbitrary traits in polygynous birds. Generally, however, the Fisher process is usually considered an intellectual curiosity (or even a monstrosity, Grafen 1990) of little relevance to real organisms.

The LK model has been almost universally rejected as empirically irrelevant because it has been inappropriately treated as an alternative hypothesis instead of as the null hypothesis. Grafen's (1990) requirement of "abundant proof" before accepting the Fisher–LK process constitutes demanding an impossibility—proof of the null hypothesis. Because natural selection on mating preferences is frequently assumed a priori, the burden of proof has been placed inappropriately on the LK null model to demonstrate that natural selection on mating preferences does not exist. Currently, one cannot state in the literature that a display trait is arbitrary unless one has rejected all the possible adaptive signaling and efficient signaling hypotheses. [I know having experienced exactly this argument in peer review.] Of course, the completely generalized hypothesis that a phenotypic feature is an adaptation is unfalsifiable given that one can always imagine another possible adaptive function that has yet to be tested. Thus, current intellectual framework of intersexual selection research is structured to prevent recognition of any role for a null sexual selection process. Recognition of the LK null intersexual selection model would place the burden of proof on researchers to demonstrate that the critical parameters are not equal to zero (Appendix).

Although most investigators assume that the existence of searching and mating costs supports the existence of natural selection on mating preferences, the general viability costs of mate searching and mating itself should not be confused with the specific viability costs of alternative mating preferences and

alternative mates. The relevant issue is not whether there are any costs to mate searching and mating in general, but whether there are *specific differential costs* to the heritable variations in mating preference within a population. The existence of the former is not evidence of the latter. Of course, variation in mating preferences is difficult enough to document in wild populations; it will be substantially harder to measure whether mating preferences are actually under natural selection. However, this is exactly the work that needs to be done to establish the importance of natural selection on mating preferences.

Likewise, the existence of trait production costs and trait survival costs are often used as evidence of the evolution of honest quality information in trait variation through either indirect or direct benefits. The existence of trait production or survival costs, however, does not constitute evidence: (1) that such costs are differentially higher on lower quality individuals, as handicap models require (e.g., Grafen 1990), (2) that condition-dependent trait variation is correlated with heritable, additive genetic variation in viability in addition to the direct effects of the trait, and thus (3) that the signals evolved through natural selection to encode condition-dependent variation. The LK null model also predicts the evolution of trait values that are far from the natural selection optimum. Under these conditions, males should be expected to incur both trait expression costs and survival costs. But, such trait costs are not automatically correlated with heritable genetic components of viability in addition to the direct viability costs of the trait itself, and thus would not necessarily evolve through natural selection on preference. Thus, the existence of costly display traits does not necessarily falsify the null Fisher process.

Other qualities of courtship display performance, including vigor, motor skill, and signal complexity, have also been hypothesized to have evolved to provide females with reliable quality information (Byers et al. 2010). However, there is no reason that display vigor, skill, and complexity would not be expected to evolve through null LK sexual selection mechanism alone. The issue is whether vigor, skillful performance, and complexity evolve as an incidental byproduct of the coevolution of display traits and mating preferences, or if these features are the direct object of female mating preferences shaped by adaptive natural selection for the expression of specific quality information. We cannot assume the latter is true just because the adaptationist account is more intellectually fashionable.

Similarly, a significant correlation between secondary sexual traits and the sensory environment (e.g., display coloration and the visual background) does not mean that such an association has evolved by natural selection on mating preferences for mate-search efficiency. Although explicit mathematical models have not attempted to demonstrate this, it is clear that arbitrary mating preferences for specific combinations of traits and sensory environments could easily evolve in the absence of natural selection

on preferences for sensory efficiency. Just because a signal stands out efficiently from the sensory background, it does not mean that it has evolved by natural selection on preferences to do so. There is nothing in the null LK process that would restrict the evolution of a preference for an arbitrary trait with a highly specific relationship to its sensory background. Stop signs use red and white to stand out efficiently from the sensory background, but mating preferences for an identical signal-to-background color contrast could evolve through a purely arbitrary null sexual selection process: for example, the brilliant male of the sexually dimorphic Scarlet-and-white Tanager (*Chrysopthlypis salmoni*, Thraupidae) of western Ecuador and Colombia (Ridgely and Tudor 1989). Given that most sensory environments are highly nonarbitrary, the null prediction should be that most arbitrary traits should stand out from the sensory background in dramatic ways that may enhance sensory efficiency. Thus, neither trait costs nor trait correlations with the sensory environment are exclusive predictions of adaptive mate choice models.

Another red herring commonly deployed in discussions of the plausibility of the Fisherian and LK null model is that they cannot explain that origin of mating preferences themselves. Although this is theoretically true, it is likely to be irrelevant to the investigation of sexual selection in most living species. For example, among the >10,000 species of birds, none is known to entirely lack secondary sexual display indicative of the existence of mating preferences. Thus, mating preferences of birds very likely evolved prior to the origin and radiation of living birds in a lineage of theropod dinosaurs in the Jurassic (Prum 2002, 2008). If, by conservative estimate, the mating preferences of all modern birds originated prior to the breakup of Gondwanaland, then the theoretical concerns about the origin of mating preferences provide no constraint whatever on the application of the LK mechanisms to species and populations of living birds.

Although most current researchers think that the LK mechanism is extremely unlikely in nature, some prominent evolutionary biologists have concluded otherwise. Maynard Smith wrote that "symbols [=arbitrary traits] seem to be common in mate choice. This is to be expected if the evolutionary mechanism is that of Fisher (1930): all that is required is an initial arbitrary preference by some females later exploited by males" (Maynard Smith and Harper 2003: 59). Although this brief statement is the only substantive comment on the Fisher process in an entire book on the evolution of communication, it confirms that if one takes null mechanisms of sexual selection seriously, one is lead to the conclusion that arbitrary traits are likely to be common.

The LK Null and Trait Evolvability

Incorporating an appropriate null model into intersexual selection research would have the enormously beneficial effect of

advancing hypothesis testing over confirmationism in evolutionary biology. Unlike Hardy–Weinberg, however, an additional benefit is that the null hypothesis of evolution by intersexual selection might frequently be true. Serious empirical consideration of LK sexual selection mechanism has been so rare, that few researchers have actually considered what an arbitrary trait/preference radiation would be like and how it would differ from a trait radiation in which mating preferences are under constant natural selection.

In 1997, I argued that the "Fisherian" process (equivalent to the null LK model here) makes distinct macroevolutionary predictions about the patterns and rate of male trait diversification (Prum 1997). Specifically, natural selection on preference should constrain the evolution of trait diversity among lineages. In brief, direct benefit and good genes models function through a positive correlation between trait values and viability (e.g., Kokko et al. 2006). This quality correlation either has to either exist a priori, or it has to evolve. Such a quality correlation can only evolve if those components of genetic variation for the trait that are not correlated with quality are eliminated by sexual selection on the trait. As a simplistic example, in order for tail length to indicate genetic quality, diet quality, or ability to invest in parental care, there cannot exist a lot of genetic variation for tail length that is uncorrelated with these variables. Ultimately, as Fuller et al. (2005) and Kokko et al. (2006) point out, the indicator trait may evolve to lack all genetic variation, leaving only genes that encode for condition-determined expression. However, the genetic conditions resulting from the evolution of intersexual signal honesty—no additive genetic variation—are exactly those under which a display trait will be constrained from evolving. Thus, to the extent mating preferences evolve for honest indicators, the evolvability of traits and preferences will be constrained within and among populations (Prum 1997). Furthermore, given that there are relatively few components of the phenotype that could possibly evolve condition-determined expression, there should be extensive convergence in display traits among clades, further reducing the diversifying consequences of sexual selection (Prum 1997). Robust honesty and its consequent constraints on evolvability have been specifically proposed as an advantage of honest indicators. For example, Hamilton and Zuk (1982) proposed that bright plumage evolves to be a consistent and robust indicator of resistance to rapidly coevolving parasites. Female mate choice on the basis of such traits would lead to the evolution of consistently fitter, but not brighter, mates.

The evolution of a repertoire of multiple costly display traits will be further constrained by natural selection on preferences (e.g., Iwasa and Pomiankowski 1994). To provide new information about quality or condition, new indicator traits need to have additional expression or viability costs. Consequently, new indicator traits can only evolve if they communicate an orthogonal dimension of quality information, providing a substantial hurdle to the evolution of new traits to a repertoire (Iwasa and Pomiankowski 1994). As display repertoire increases, the possibility that each new display trait can communicate additional, orthogonal information about viability diminishes, further constraining repertoire evolution (Prum 1997). In contrast, the LK null model incorporates numerous opportunities for unrestricted trait elaboration and repertoire (e.g., Pomiankowski and Iwasa 1993). Thus, natural selection on mating preferences will constrain the evolvability of secondary sexual traits repertoires relative to the null LK mechanism.

In summary, the null LK model makes radically different predictions about the evolvability of intersexual display traits from those of adaptive mechanisms of mate choice. Essentially, adaptive mate choice models will constrain trait evolvability, whereas the null LK mechanism will greatly foster it. If natural selection on mating preferences drives trait evolution, then the diversity of radiations of secondary sexual traits should look like adaptive radiations of other traits under natural selection—such as cryptic plumage coloration, call notes, and beak shapes. Of course, it has been obvious since Darwin (1871) that this is not the case.

Prum (1997) proposed the polygynous, lekking manakins (Pipridae) as an example of Fisherian radiation in secondary sexual traits. This Neotropical clade of ∼45 lekking species features numerous, diverse secondary sexual plumage, behavioral, and vocal traits (Prum 1990b, 1994; Snow 2004). Females have plumage of slightly variable shades of green; males of most species are brightly color patterned and perform elaborate courtship displays. In contrast, a possible example of an evolutionary radiation of honest indicator signals could be the Holarctic genus *Carpodacus* (Fringillidae). A series of now classic studies of the House Finch (*Carpodacus mexicanus*) have shown that the carotenoid patches are condition-dependent indicators of dietary carotenoid content (reviewed in Hill 2002; Hill 2006). The ∼40 socially monogamous species of *Carpodacus* are characterized by similarly, drab brown plumaged females and bright males with red, carotenoid-pigmented plumage patches on their heads, breasts, and rumps. In a striking contrast with manakins, male plumages of different species of *Carpodacus* from Europe, the Himalayas, Canada, the Rockies, and New England are strikingly similar, and constitute some of the most difficult to identify brightly plumaged birds. The striking difference between the manakin and *Carpodacus* finch secondary sexual trait radiations implies that something different is going on in the two clades. Given the striking diversity in outcomes of sexual selection in different organisms, we need to recognize that the prior probability of natural selection on mating preferences is not always identical to one.

Of course, the evolutionary conclusions one can derive from this comparison will be dependent on the phylogeny of these organisms. Although the monophyly of manakins (Pipridae) is not in doubt (Prum 1990a, 1992; Tello et al. 2009), recent literature

indicates that *Carpodacus* may be polyphyletic. The Asian and North American clades of *Carpodacus* may not be closely related within finches (Arnaiz-Villena et al. 2007). Although this result does undermine the comparison I propose between this pseudo-radiation and the lekking manakins, such a striking example of convergence in the evolution of a proposed condition-dependent, secondary sexual signal system is strongly congruent with the hypothesis that selection for honest condition-dependent trait expression will foster convergent evolution among clades (Prum 1997).

Intersexual Selection Without a Null Model

Without an appropriate null model, the goal of intersexual research becomes merely to confirm the effects of natural selection on mating preferences for mate quality or sensory efficiency. Here, I discuss recent examples sexual selection research in the absence of a null model. Because genuine consideration of null intersexual selection models has been so rare, this review could potentially include nearly all empirical studies of intersexual selection. However, I will focus on a few examples that illustrate the pitfalls of the confirmationist approach. By focusing on diverse examples from a single clade—the birds—that has been extensively studied, I document how the absence of a null model can distort our entire view of the evolution of the intersexual displays of a whole class of organisms.

CAROTENOID VERSUS MELANIN PLUMAGE COLORATION

McGraw, Hill, and others have hypothesized that avian plumage color signals based on exogenous carotenoid pigments are more likely to exhibit condition-dependent honesty than signals based on endogenous melanin pigments (Hill 2006; McGraw 2006a, b). Griffith et al. (2006) challenged this hypothesis with a meta-analysis of studies of condition dependence in carotenoid- and melanin-based avian plumage patches. The meta-analyses included 18 published studies on melanin and carotenoid plumage signals from 12 socially monogamous bird species. They concluded that there was no evidence of a difference in condition dependence between carotenoid and melanin traits, and that both are condition-dependent indicator signals. Although Griffith et al. (2006: 759) exhorted their readers to "to tackle [these questions] from as broad a perspective as possible," they never entertained the possibility that that neither carotenoid nor melanin signals in avian plumages are condition dependent.

Griffith et al.'s (2006) analysis may be a better indication of the power of the idea of natural selection on the judgment of biologists than on avian mating preferences for plumage coloration.

To their credit, following Palmer (1999), Griffith et al. presented "funnel graphs" of effect size versus sample size and documented the severe publication bias against small sample sizes. However, their funnel graphs also document a conspicuous publication bias against negative effect sizes that contradict the hypothesis of positive condition dependence. Griffith et al. did not follow Palmer's (1999) recommended procedure for identifying the true effect size by assuming a normal distribution of random sampling error and a decrease in random error with sample size. Following these criteria, Griffith et al.'s data indicate that the true effect sizes for both carotenoid and melanin variation and condition are indistinguishable from zero (compare Fig. 2 of Griffith et al. [2006] to Fig. 1 of Palmer [1999]).

Thus, Griffith et al. (2006) meta-analysis documents exactly the opposite of what they concluded. Neither carotenoid nor melanin pigments demonstrated any significant pattern of condition dependence in their meta-analysis. Their analysis confirmed the strength of the selection they had assumed. This result might not be too surprising given that evidence of carotenoid limitation in the diets of wild birds—a fundamental assumption of honest carotenoid signaling—comes from only a single study of House Finches (Hill et al. 2002). Without irony, Griffith et al. (2006: 760) conclude, "Selection is a very powerful force and we should not underestimate its ability to produce an honest signal out of whatever is available, regardless of what we may think about the biological and physiological suitability of different pigments or structures" (Griffith et al. 2006: 760).

PLUMAGE COLOR RADIATION IN A POLYGYNOUS CLADE

Doucet et al. (2007) analyzed the evolution of color signals in the manakins (Pipridae) with spectrophotometry and quantitative visual analysis of sexual dimorphism in plumage color and brightness, and using the phylogeny from Prum (1997). However, they made no attempt to test Prum's (1997) hypothesis of a Fisherian (=null LK) radiation in the manakins. Rather, they produced an analysis that merely confirms their view that male plumage coloration in manakins has evolved through natural selection on mating preferences to an optimal balance between honesty and efficiency.

Doucet et al. (2007) used color contrast between the sexes as their measure of the strength of sexual selection. They showed that sexual color contrast was positively correlated with chromatic and achromatic contrast from the green forest background for males but not for females. They concluded that, "our findings suggest that sexual selection has favored the evolution of conspicuous plumage ornaments that enhance signal efficacy in male manakins by creating high visual contrast against the background" (Doucet et al. 2007: S75). Of course, female manakin plumages are subtle variations on green that strongly match the visual background.

Any sexual dimorphism in color would necessarily support the adaptive hypothesis of efficient signaling through natural selection on preferences. Sexual dimorphism in color has been defined a priori as an adaptation that will confirm the hypothesis of natural selection for efficient signaling.

Doucet et al. (2007) then show that among plumage patch color and brightness contrast within male plumages is positively correlated with sexual dimorphism (again their measure of intersexual selection). They assert that, "by increasing contrast between plumage patches, male manakins become more conspicuous to nearby females but not necessarily to distant predators. Thus, the evolution of multiple colored plumage patches may offer a partial resolution of the conflict between selection for conspicuous intraspecific sexual displays and selection for predation avoidance through crypsis" (Doucet et al. 2007: S76). There is no surprise, however, that the occurrence of multiple male color patches is positively associated with sexual dimorphism because each additional patch provides an opportunity to be more different from female-like green. Again, Doucet et al. (2007) have constructed an analysis in which any deviation from sexual monochromatism supports a specific adaptive mate choice hypothesis.

Lastly, Doucet et al. (2007) show that different plumage coloration mechanisms—that is, different types of pigments and structural coloration—produce different average levels of chromatic and achromatic contrast with the green background. They argue that, because different color mechanisms have different potential to express condition dependence (see above), variation in the color of different color mechanisms creates evolutionary trade-offs between signal efficacy (i.e., difference from green) and signal information content (i.e., male condition). The analysis rests on the unsupported assumption that carotenoids are limited in the diets of tropical forest frugivores, even though tropical fruits are known to be conspicuously high in carotenoids (e.g., Goodwin 1980; Mangels et al. 1993). Doucet et al. (2007) then claim that the existence of variation in color contrast produced by different coloration mechanisms is evidence of the existence of the hypothesized trade-offs. The biological fact that plumage colors are produced by multiple distinct physical mechanisms with different intrinsic physiological properties is cited as evidence in support of adaptive trade-offs themselves.

In the absence of any null hypothesis, Doucet et al. (2007) have interpreted multiple details of the radiation in male manakin plumage color as supporting the crucial role of natural selection on female mating preferences in the evolution of this radiation. Differences in male plumage color from leafy, female-like green are evidence of signal efficiency. Variations among male color patches are evidence of an optimal balance between signal design and direct natural selection. Variations among coloration mechanisms are evidence of adaptive trade-offs between signal efficiency and honesty. But the analyses have been constructed

to confirm these adaptive mate choice hypotheses rather than test them. Doucet et al.'s conclusions are based on the existence of: (1) sexual dichromatism and female crypsis, (2) multiple male color patches, and (3) multiple physical and pigmentary coloration mechanisms. Because sexual dimorphism, multiple color patches, and variation among plumage color mechanisms are all entirely consistent with the null LK sexual selection model, Doucet et al. (2007) provide no evidence in conflict with the conclusion that male manakin intersexual display traits are an arbitrary Fisherian (=LK) radiation (Prum 1997).

SONG

Bird song is an example of an extremely diverse and complex form of communication that is frequently under intersexual selection (e.g., Searcy and Nowicki 2005). Much of the recent literature on intersexual selection in bird song explores adaptive, honest signal content in vocal communication in the absence of any null hypothesis (Searcy and Nowicki 2005). For example, Gil and Gahr (2002) explore how diverse aspects of avian vocal behavior—including vocal performance, repertoire size, song content, song timing, counter-singing patterns, etc.—are each subject to costly production constraints that will enforce signal honesty. However, their review of the evidence of honest signaling revealed mixed to poor support for honest quality information for each of these features. For example, although song repertoire size has frequently been hypothesized to indicate male neural capacity and, thus, mate quality, most field studies have found a poor correlation between repertoire size and pairing success when controlled for territory quality and arrival date (Gil and Gahr 2002). Gil and Gahr did even not discuss the evidence of phylogenetically derived reductions in song repertoire size in *Zonotrichia* sparrows (Emberizidae)(Irwin 1988) which directly challenge this hypothesis.

Despite their disappointing results, Gil and Gahr (2002) remain ardently optimistic that natural selection on mating preferences will create quality information in vocal signals. Failure to confirm the signal of natural selection on vocal mating preferences is interpreted as evidence of not having looked hard enough. They conclude that the evidence of vocal honesty remains illusive because of the inherent complexity of avian vocal behavior. They never consider whether the predictions of honest signaling have been repeatedly falsified. They never attempt to explain the evolution of those variations in vocal variation that do not fit the honest signaling hypothesis. For example, once song repertoire size fails to confirm the hypothesis of signal honesty, Gil and Gahr loose interest in the scientific explanation of its dynamic evolutionary history and move on to other speculations on the elusive honesty of other aspects of vocal complexity. In the absence of a null model, confirmation of natural selection's role in evolution of mating preferences has replaced the more fundamental job of scientific explanation itself.

Failure to support signal honesty can also result in the proposal of specific ad hoc hypotheses that allow for evasion of falsification. For example, Nowicki et al. (1998) were puzzled by the same absence of support for the hypothesis that song repertoire size is an honest indicator of quality. Rather than reject the hypothesis and attempt another general explanation of repertoire size evolution, however, Nowicki et al. proposed the ad hoc hypothesis that small song repertoires also provide honest information about male quality by demonstrating the ability to learn with high fidelity and to sing repeatably with low variance. Here, failure to support the adaptive hypothesis spawned a Panglossian auxillary hypothesis that maintains the plausibility of adaptive signal honesty.

Conclusion

Empirically, we cannot assume that natural selection on preferences always exists, and then design research to discover that the details of this "fact." Rather, we should adopt a null model of intersexual selection and test whether we can reject its predictions.

More theoretical work needs to be done to understand the full microevolutionary and macroevolutionary implications of the null sexual selection process, and to develop theory that explicitly examines the independent testable predictions of adaptive mate choice models. Unfortunately for those with little interest in it, the LK process generates broad and diverse microevolutionary (Lande 1981; Kirkpatrick 1982) and macroevolutionary (West-Eberhard 1983; Prum 1997) predictions. As Fisher recognized, the intrinsic evolutionary consequences of the existence of genetic variation for mating preferences and traits encompass an amazing richness of arbitrary evolutionary outcomes.

How do we incorporate the LK null model into intersexual selection? Unlike the Hardy–Weinberg equilibrium, the predictions of the LK process do not provide a single, simple test for the existence of natural selection on mating preferences. Researchers must test those hypotheses that actually distinguish the null model from adaptive mate choice models. For example, direct evidence of natural selection on variations in mating preferences for specific display trait values—not merely costs of mate searching in general—would falsify the LK null model. The existence of trait production costs, survival costs, and trait correlations with sensory environment are also entirely consistent with the null sexual selection model. Display vigor, skill, and complexity are predictable outcomes of the null LK mechanism. Evidence of disproportionally higher trait production or viability costs on lower quality males would support an exclusive prediction of honest signaling models (Grafen 1990). I do know of any attempts to test this fundamental assumption of honest intersexual signaling models. The presence of a genetic correlation between trait and preference has been viewed as a testable prediction of the LK process, however it may be practically impossible to detect a significant trait/preference genetic correlation in a population at equilibrium when the genetic correlation may be within measurement error.

It has been convenient to discredit the null LK mechanism a priori, and avoid taking the intrinsic consequences of genetic variation in traits and preferences seriously. The view that Fisherian–LK mechanism are perverse or even "methodologically wicked" (Grafen 1990: 487) has been so successful precisely because it demands the impossible–-proof of the null hypothesis. One cannot prove that a trait is arbitrary. One can only demonstrate that a trait is consistent with the predictions of the arbitrary null model or falsify that claim. Incorporation of an LK null model in sexual selection means that when we fail to reject the null model, we should accept the arbitrary LK process as the best explanation of the data. This is especially true in instances in which the prior probability of natural selection on mating preferences is obviously not one: for example, in polygynous species in which males contribute only sperm to reproduction.

It is tempting, but unscientific, to assume the role of natural selection a priori in the evolution of any specific instance of a derived trait, phenotypic feature, or genetic change. The efficiency of natural selection as an evolutionary mechanism is beyond doubt, but different individual hypotheses of adaptive evolutionary change still require testing. Taxa, populations, and organisms are ontological individuals with their own spatiotemporal restrictions (Ghiselin 1987), and organic evolution is not the product of deterministic laws (Beatty 2006; but see Sober 2006b). Those interested in the role of natural selection on mate preferences in sexual selection should have no resistance to adopting the null model framework proposed here, just as those interested in natural selection on genetic variation consistently use neutral genetic theory. An important consequence, however, is that our general conclusion that arbitrary process is irrelevant to nature will now be subject to empirical evaluation.

I do not claim that the "Emperor wears no clothes." Rather, I would predict that the "Emperor wears a loincloth." I estimate that the adaptive signaling paradigm covers about the same proportion of the total corpus of intersexual signals as does that humble garment. I predict that the majority of intersexual traits and mating preferences are arbitrary. They have gone unexamined and unexplained because they do not conform to current intellectual fashion. To me, the expansively arbitrary signal diversity predicted by the null LK mechanism looks a lot like the overwhelming, multidimensional diversity of the secondary sexual display traits in nature. Is this account anywhere near accurate? Currently, intersexual selection research is structured to prevent us from being able to find out. Adopting the LK mechanism as the null model in intersexual selection will permit us to do so for the first time.

How common will arbitrary intersexual signals be? Macroevolutionary models of null and adaptive sexual selection mechanisms have not been developed to make quantitative predictions. By analogy, however, we can examine the frequency of arbitrary signals in a different complex, coevolved communication system: spoken human language. In language, the vast majority of words are arbitrary associations between a set of phonemes and their culturally coevolved meanings. The overwhelming majority of all words—such as table, floor, and ferruginous—are arbitrary in phonetic form with respect to their meaning. Only a small proportion of all possible words actually encode their meanings through their variations in form. Onomatopoetic words—such as pop, splat, murmur, and hoopoe—encode their actual meanings in their phonemes. Another unusual example of a word that encodes its own meaning is the English word sesquipedalian, which means "someone who likes to use long words." Sesquipedalian was coined sarcastically in Latin by Horace in 97 BCE from a phrase meaning "measures one foot and a half long" (Oxford English Dictionary 2005). Arbitrary words comprise the overwhelming majority of all languages, whereas words whose form encodes their meanings are vanishingly rare by comparison. Intersexual selection research programs that intellectually structures so as to prevent the identification of arbitrary traits may resemble a linguistics of onomatopoeia—a distorted cartoon of biodiversity.

This debate is as old as sexual selection theory itself. Cronin (1991) provides an insightful historical analysis of the debate between Charles Darwin and Alfred Russell Wallace over evolution by mate choice. Darwin proposed that display traits evolve purely for the "aesthetic" delight of the female's "taste for the beautiful." Despite a few ambiguous passages, Darwin (1871) was clear that mate choice created a distinct evolutionary process with different outcomes than natural selection. Despite his lengthy arguments that evolution by mate choice was unlikely, Wallace never completely rejected it (Cronin 1991). Rather, Wallace maintained that mate choice could not lead to any independent evolutionary dynamics distinct from those created natural selection itself, and that the evolutionary consequences of mating preferences would be constantly reined in by, and serve the purposes of, natural selection. In a passage entitled "*Natural Selection as neutralising Sexual Selection*," Wallace (1895:378–9) wrote, "The only way in which we can account for the observed facts is, by the supposition that colour and ornament are strictly correlated with health, vigour, and general fitness to survive." Wallace's view could come from a contemporary defense of adaptive mate choice models. Of course, Wallace's skeptical view prevailed and intersexual selection was consequently abandoned for an entire century.

Few recognize, as Cronin (1991) documents, that the contemporary dominance of adaptive intersexual selection models, which assume a controlling power of natural selection on mating preferences, represents a triumph of Wallace's view over the arguments of Darwin himself. Most contemporary researchers are the intellectual descendents of Wallace. Like Wallace, they are using the logic of Darwin's *Origin* to argue against Darwin's *Selection in Relation to Sex*. For one, Dawkins (2004: 265–266) proudly embraces Cronin's label as a modern Wallacean, describing the theories of Zahavi, Hamilton, and Grafen as a "neo-Wallacean" triumph over the incomplete and muddled mate choice mechanism of Darwin and Fisher. Other modern researchers are obscuring their Wallacean roots. By redefining various sources of natural selection on mating preferences as sexual selection (Fuller et al. 2005; Kokko et al. 2006), current sexual selection theory completes the conversion of sexual selection into a Wallacean theory with a distinctly new spin. Whereas Wallace proposed that natural selection should control and dictate the evolutionary consequences of mating preferences, he called this combined process natural selection. Neo-Wallaceans agree entirely except that they now call this combined theory sexual selection.

In future work, I will argue further that Darwin's explicitly aesthetic view of the intersexual selection are exactly congruent with the Fisherian and LK null models. Adoption of the null LK model of evolution by intersexual selection will allow us to return to the Darwin–Wallace debate about the relative role of natural and sexual selection in the mate choice with new empirical focus.

There are striking parallels between the current state of intersexual selection and the recent intellectual history of macroeconomics. The contemporary global financial crisis was greatly fostered by the unquestioned belief in the efficient market hypothesis that states that the price of assets will be driven to their true intrinsic value by rational choice in a free market (Krugman 2009). The irrational exuberance of a financial market bubble—which bears remarkable mathematical resemblance to a Fisherian runaway—was deemed theoretically impossible, indeed indefinable, by the efficient market hypothesis (Krugman 2009). The categorical denials of a housing market bubble by efficient market enthusiasts of "Panglossian finance" (Krugman 2009) are strikingly similar to the intemperate rejections of the plausibility of a Fisherian or LK mechanisms that populate the contemporary intersexual selection literature (e.g., Grafen 1990). We all now know how well dogmatic belief in the efficient market hypothesis worked out.

The histories of community ecology and evolutionary genetics demonstrate the intellectual pitfalls of lacking an explicit null hypothesis. Despite years of debate and resistance to their application, null and neutral models are now essential to research in both these fields. From the intellectual histories of these disciplines, evolutionary biologists should recognize that it will be intellectually responsible and productive to incorporate the LK null model in to intersexual selection. To paraphrase Felsenstein's (1985) famous defense of phylogenetic comparative methods, the LK

mechanism is fundamental to intersexual selection, and there is no studying intersexual selection without taking it into account.

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Appendix

A Quantitative Genetic LK Null Model

To clarify the definition of the LK mechanism as the null model of evolution by intersexual selection, the LK conditions are explicitly defined here using the generalized quantitative genetic model of Fuller et al. (2005). Drawing on decades of advances following Lande's (1981) framework, Fuller et al. (2005) modeled the change in mean population phenotype a display trait t, a mating preference p, and the heritable genetic components of viability v (or "naturally selected fitness including variation in fecundity but not affected by mate quality or number"). The vector of change in the mean of these three phenotypic features, denoted $\Delta\bar{\mathbf{z}}$, is product of the genetic variance–covariance matrix, $\mathbf{G}$, and a vector of selection gradients, $\boldsymbol{\beta}$, plus a vector of mutational effects, $\mathbf{u}$

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\boldsymbol{\beta} + \mathbf{u}.$$

The selection gradient vector $\boldsymbol{\beta}$ is decomposed into the sum of components due to natural selection, $\boldsymbol{\beta}_N$, and sexual selection, $\boldsymbol{\beta}_S$

$$\Delta\bar{\mathbf{z}} = \mathbf{G} \times (\boldsymbol{\beta}_N + \boldsymbol{\beta}_S) + \mathbf{u}.$$

Expanding $\Delta\bar{\mathbf{z}}$, $\mathbf{G}$, $\boldsymbol{\beta}$, and $\mathbf{u}$ gives

$$\Delta\bar{\mathbf{z}} = \begin{pmatrix} \Delta\bar{t} \\ \Delta\bar{p} \\ \Delta\bar{v} \end{pmatrix} = \begin{pmatrix} V_t & C_{tp} & C_{tv} \\ C_{tp} & V_p & C_{pv} \\ C_{tv} & C_{pv} & V_v \end{pmatrix} \\ \times \left(\begin{bmatrix} \beta_{Nt} \\ \beta_{Np} \\ \beta_{Nv} \end{bmatrix} + \begin{bmatrix} \beta_{St} \\ \beta_{Sp} \\ \beta_{Sv} \end{bmatrix} \right) + \begin{bmatrix} u_t \\ u_p \\ u_v \end{bmatrix},$$

where V is additive genetic variance of trait, preference, and viability; and C is genetic covariance between trait, preference, and viability.

The general conditions for the LK null model are given by

$$
\begin{pmatrix} \Delta \bar{t} \\ \Delta \bar{p} \\ \Delta \bar{v} \end{pmatrix} = \begin{pmatrix} V_t > 0 & C_{tp} > 0 & C_{tv} \equiv 0 \\ C_{tp} > 0 & V_p > 0 & C_{pv} \equiv 0 \\ C_{tv} \equiv 0 & C_{pv} \equiv 0 & V_v \end{pmatrix}
$$
$$
\times \left(\begin{bmatrix} \beta_{Nt} \\ \beta_{Np} \equiv 0 \\ \beta_{Nv} \end{bmatrix} + \begin{bmatrix} \beta_{St} \neq 0 \\ \beta_{Sp} \equiv 0 \\ \beta_{Sv} \end{bmatrix} \right) + \begin{bmatrix} u_t \\ u_p \\ u_v \end{bmatrix}.
$$

The key features of the LK conditions are that: the additive genetic variance of the display trait and mating preference are both positive ($V_t > 0$, $V_p > 0$); the genetic covariances between the trait and viability is zero for all values of the trait ($C_{tv} \equiv 0$); the genetic covariance between preference and viability is zero for all values of the preference ($C_{pv} \equiv 0$); direct sexual selection on the display trait through the expression of the mating preference is nonzero ($\beta_{St} \neq 0$); and all other direct natural and sexual selection on preference is zero for all values of preference ($\beta_{Np} \equiv 0$; $\beta_{Sp} \equiv 0$).

In the LK process, the genetic covariance between trait and preferences ($C_{tp} > 0$) evolves as a consequence of selective mating, and is an intrinsic consequence of genetic variation in trait and preference ($V_t > 0$, $V_p > 0$). Preference evolves indirectly through the sexual selection it creates on the display trait (β_{St}) and its genetic covariation with the trait ($C_{tp} > 0$). Natural selection on the display trait can occur during the LK process, but is not necessary ($\beta_{Nt} \geq 0$). If natural selection on the display trait does occur ($\beta_{Nt} > 0$), then an equilibrium condition exists in which sexual selection on the trait is balanced by natural selection on the trait ($\beta_{Nt} = -\beta_{St}$; $\beta_{St} = -\beta_{Nt}$)(Fig. 1A)

$$
\begin{pmatrix} \Delta \bar{t} \\ \Delta \bar{p} \\ \Delta \bar{v} \end{pmatrix} = \begin{pmatrix} V_t > 0 & C_{tp} > 0 & C_{tv} \equiv 0 \\ C_{tp} > 0 & V_p > 0 & C_{pv} \equiv 0 \\ C_{tv} \equiv 0 & C_{pv} \equiv 0 & V_v \end{pmatrix}
$$

$$
\times \left(\begin{bmatrix} \beta_{Nt} = -\beta_{St} \\ \beta_{Np} \equiv 0 \\ \beta_{Nv} \end{bmatrix} + \begin{bmatrix} \beta_{St} = -\beta_{Nt} \\ \beta_{Sp} \equiv 0 \\ \beta_{Sv} \end{bmatrix} \right) + \begin{bmatrix} u_t \\ u_p \\ u_v \end{bmatrix}.
$$

The model produces a line of equilibrium combinations in mean trait and preference that is between sexual and natural selection on the trait (Fig. 1A) (Lande 1981). The stability of the evolutionary equilibrium will be determined by the slope of the evolutionary trajectory lines, or V_t / C_{tp}. If $C_{tp} < V_t$, then p will only evolve a little bit with evolutionary change in the t, and the population will evolve toward a point on the stable line of equilibria (Fig. 1B). If $C_{tp} > V_t$, then evolutionary change in p will be large for small changes in t, then all equilibria are unstable and the population will evolve rapidly toward increasingly extreme combinations of mean trait and preference (Fig. 1C). Which conditions occur will be determined in part by the relative magnitude of the mutational effects on the trait and the preference (u_t and u_p). For populations at a stable equilibrium, genetic drift in trait and preference will lead to evolution of new equilibria resulting in increased differentiation in trait and preference combinations.

In contrast to the LK null model conditions, all other models of intersexual selection require that some additional parameters have values $\neq 0$. Indirect selection for good genes occurs when there are positive covariances between trait and viability ($C_{tv} > 0$) and preference and viability ($C_{pv} > 0$) but no sexual selection on preference ($\beta_{Sp} \equiv 0$). In the Fuller et al. (2005) framework, selection for various direct benefits involves sexual selection on preference ($\beta_{Sp} \neq 0$), and sensory bias occurs when natural selection on preferences (i.e., natural selection on preferences for features unrelated to mate choice) is positive ($\beta_{Np} \neq 0$) but selection on preference for features concerning male quality are zero ($\beta_{Sp} \equiv 0$). See Fuller et al. (2005) and Kokko et al. (2006) for more details.