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Review

Aesthetic evolution by mate choice: Darwin's *really* dangerous idea

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Darwin proposed an explicitly aesthetic theory of sexual selection in which he described mate preferences as a 'taste for the beautiful', an 'aesthetic capacity', etc. These statements were not merely colourful Victorian mannerisms, but explicit expressions of Darwin's hypothesis that mate preferences can evolve for arbitrarily attractive traits that do not provide any additional benefits to mate choice. In his critique of Darwin, A. R. Wallace proposed an entirely modern mechanism of mate preference evolution through the correlation of display traits with male vigour or viability, but he called this mechanism natural selection. Wallace's honest advertisement proposal was stridently anti-Darwinian and anti-aesthetic. Most modern sexual selection research relies on essentially the same Neo-Wallacean theory renamed as sexual selection. I define the process of aesthetic evolution as the evolution of a communication signal through sensory/cognitive evaluation, which is most elaborated through coevolution of the signal and its evaluation. Sensory evaluation includes the possibility that display traits do not encode information that is being assessed, but are merely preferred. A genuinely Darwinian, aesthetic theory of sexual selection requires the incorporation of the Lande–Kirkpatrick null model into sexual selection research, but also encompasses the possibility of sensory bias, good genes and direct benefits mechanisms.

Keywords: sexual selection; natural selection; aesthetics; beauty; adaptation

1. INTRODUCTION

For more than two decades, I have been interested in the role of arbitrary, Fisherian sexual selection mechanisms in the evolution of sexually dimorphic, ornamental traits in polygynous birds [1–3]. During this same period, this intellectual perspective has become increasingly marginalized within evolutionary biology. Recently, I reframed my view [4] by proposing that the Lande–Kirkpatrick (LK) mechanism of sexual selection by mate choice [5–7], which is based on Fisher's verbal model [8–10], is the appropriate null model for evolution of traits *and* preferences by intersexual selection [4]. I stated that the wholesale rejection of LK mechanism in the early 1990s has led to the rejection of testability itself [4].

The result is that the study of sexual selection has become a weak science that largely seeks to confirm the adaptive hypotheses it assumes—i.e. that natural selection on mating preferences is the determining force in intersexual selection. In this intellectual environment, failure to confirm an honest indication or adaptive signalling hypotheses merely means that the researchers have failed to work hard enough to do so. With the exception of sensory bias research programmes, the possibility that traits are not indicating anything is rarely even entertained. Sexual selection has become a field in which the role of natural selection on mating preferences is usually assumed, rarely discussed, largely beyond testing and even redefined into the definition of sexual selection itself.

The prospect of null model debate in intersexual selection will sound familiar to those with broad interests in evolutionary biology and ecology. The previous, similar debates on neutral theory in evolutionary genetics and on null models in community ecology took years to resolve. Following those historical examples, to be effective, I should repeat the same arguments over and over for a decade or more. Gradually, intellectual change will occur as the majority of the workers in the field realize that attempting to do science without a null hypothesis is underproductive at best, and unscientific or faith-based at worst. Demographic turnover will also occur as new researchers that join the field adopt the null model viewpoint, and others retire or turn to other questions. Although the LK null model publication is recent, I will not follow these historical examples. Rather, I will expand the argument substantially to address a related core issue in sexual selection that has been marginalized for over 100 years since Darwin's [11] original sexual selection proposal—the question of aesthetics.

I will document that our modern sexual selection theory is intellectually Wallacean in structure, and that it is based on some of the very same arguments that A. R. Wallace deployed in order to kill Darwin's

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One contribution of 11 to a Theme Issue 'Sexual selection, social conflict and the female perspective'.

aesthetic view of sexual selection—namely honest indication. I recommend reviving the Darwin–Wallace debate on sexual selection and the limits of natural selection in evolution.

In general, I think history of science is best left to professionals in that field. Further, I am suspicious of any argument, including my own, that one view should be preferred because it has a purer, more direct Darwinian heritage. However, the most recent and relevant scientific antecedents to the perspective I am proposing come from Darwin's *Descent of man*; so the historical analysis I present here is specifically relevant to contemporary scientific progress. Further, the historic details of Darwin's and Wallace's debate over sexual selection reveal, in a surprising stark way, that we are still engaged in the same fundamental issues [12], except that Darwin's actual opinions have rarely been considered in over a century. To incorporate Darwin's ideas into the contemporary scientific literature, I will define a process of aesthetic evolution. I propose that the integration of the LK null model into sexual selection research is required to achieve the explicitly aesthetic sexual selection theory that Darwin proposed. I will briefly discuss advantages of the LK null [4], and reject some misconceptions about its implementation in sexual selection research.

2. DARWIN'S AESTHETIC THEORY OF MATE CHOICE

The most revolutionary and challenging feature of Charles Darwin's proposed mechanism of evolution by mate choice is that it was explicitly *aesthetic*. Darwin repeatedly wrote of mating preferences as an 'aesthetic faculty' and described them as 'a taste for the beautiful'. Darwin's references to aesthetics and beauty were not analogies, or colourful Victorian mannerisms. Rather, they were central to every attempt he made to explain this proposed mechanism of evolution, and to his conception of its evolutionary consequences. Darwin's aesthetic view was central to his motivation for proposing sexual selection as a distinct evolutionary mechanism. In all the bicentennial praise for Darwin's many brilliant scientific insights, I know of no piece of writing that has specifically and enthusiastically embraced Darwin's explicitly aesthetic viewpoint. Today, Darwin's notion of an aesthetic science of mate choice is treated like a crazy aunt in the evolutionary attic. She is not to be spoken of. Here, I enthusiastically embrace Darwin's aesthetic view and encourage its adoption by the field as a whole.

Darwin was explicit, repeated and adamant in maintaining that the evolution of secondary sexual characters by mate choice was an aesthetic mechanism of evolution. For example, he wrote:

> With the great majority of animals, however, the taste for the beautiful is confined to the attractions of the opposite sex.* The sweet strains poured forth by many male birds during the season of love, are certainly admired by the females ... If female birds had been incapable of appreciating the beautiful colours, the ornaments, and voices of their male partners, all the labour and anxiety by the latter in displaying their charms before the females would have been thrown away; and this is impossible to admit. [11, p. 61]; * sentence added in second edition)
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> On the whole, birds appear to be the most aesthetic of all animals, excepting of course man, and they have nearly the same taste for the beautiful as we have. [11, p. 466]
>
> [Male birds] charm the female by vocal and instrumental music of the most varied kinds. [11, p. 466]

It is important to establish what Darwin's language meant in modern terms. Darwin lacked our modern sensitivity to avoiding anthropomorphizing his subjects. Rather, he was actively engaged in reducing the distinctions between humans and animals. But Darwin was not trying to shock his readers. He used these aesthetic terms as ordinary language without any special semantic or cultural implications. Darwin was specifically proposing that animals (mostly females) were making sensory and cognitive evaluations of display traits, and making mate choices based on those evaluations. Darwin used 'taste for the beautiful' to refer to differential behavioural response to a secondary sexual sensory stimulus. While this aspect of Darwin's opinion was highly controversial at the time [12], it is mainstream now. If that were the only issue, there would be no need for us to revive Darwin's use of aesthetic language. Our contemporary terms cover this meaning.

Darwin's use of aesthetic language, however, implied something more than merely sensory perception, evaluation and cognitive mating preference. Darwin hypothesized that the aesthetic capacities of different species evolved differences in mating preference that could be merely pleasing for their own sake and without any other value, meaning or utility. Just like the breeders of different ornamental chickens or pigeons, Darwin hypothesized that each species has evolved to it own 'standards of beauty'. In modern parlance, Darwin's proposal is that many secondary sexual ornaments are entirely arbitrary—merely successful because they are preferred, not because they provide or communicate to the female any particular information about additional benefits [4]. Darwin used aesthetic language because it carried a non-utilitarian meaning that he specifically intended. For example, Darwin wrote,

> The case of the male Argus Pheasant is eminently interesting, because it affords good evidence that the most refined beauty may serve as a sexual charm, and for no other purpose. [11, p. 516]

This non-utilitarian result of sexual selection was in direct contrast to utilitarian natural selection, which is exactly why Darwin proposed that they are separate evolutionary mechanisms. He wrote:

> The Duke of Argyll, in commenting on this case [the unusual tail spots of a male hummingbird, *Urosticte benjamina*] ... asks, 'What explanation does the law of natural selection give of such specific varieties as these?' He answers, 'none whatever;' and I quite agree with him. [11, p. 570]

So, some of the features of Darwin's aesthetic language, which irritate contemporary readers, relate to scientific hypotheses that he specifically intended.

As many authors have previously observed [5,6,8–10,12–15], Darwin was clear that his mechanism of sexual selection could give rise to arbitrary traits. His book is filled with examples of the evolution of distinct 'standards of beauty' in different species or populations. To Darwin, these differences evolve not through any correlation with environmental factors, but through the action of mate choice itself intrinsic to each independent population.

Darwin's aesthetic view of sexual selection was also explicitly *coevolutionary.* Darwin conceived that display traits and mating preferences frequently evolved together through a mutual historical process. For example, he wrote:

> ...the male Argus Pheasant acquired his beauty gradually through the preference of the females during many generations for the more highly ornamented males; the aesthetic capacity of females advanced through exercise or habit just as our own taste is gradually improved. [11, p. 793]

By modern standards, Darwin's description of the coevolution of trait and preference is quite imprecise, but it is no worse than his explanations of the mechanisms of natural selection in the absence of a theory of genetics, which are largely viewed as being brilliantly prescient.

Darwin thought that secondary sexual display traits could express desirable qualities in a potential mate (like vigour and health), and be desirable qualities in and of themselves without communicating any special meaning or information content. In Darwin's view, the aesthetic nature of sexual selection included both of these possibilities—the arbitrary and the utilitarian. But Darwin was adamant that sexual selection could not be reduced entirely to utilitarian traits that express qualities that females will benefit from, which is why he defined it as distinct from natural selection. For example, in passages about the strength and vigour of displaying males preferred by females, Darwin wrote simultaneously of the advantages of vigour and the benefits of attractiveness, an interaction between utilitarian and purely aesthetic advantages:

> The females are most excited by, or prefer pairing with, the more ornamented males, or those which are the best songsters, or play the best antics; but it is obviously probable that they would at the same time prefer the more vigorous and lively males. Thus, the more vigorous females, which are the first to breed, will have the choice of many males; and though they may not always select the strongest or best armed, they will select those that are vigorous and well armed, and in other respects the most attractive. [11, p. 254]

Darwin's aesthetic theory included cases where female preferences were congruent with male vigour and viability, but was not entirely synonymous with them. He included both the arbitrary and the good genes/direct benefit mechanisms of mate choice, but Darwin concludes that the advantages of aesthetic beauty will dominate over mere vigour and quality.

In summary, it is a mistake for us to read Darwin as if the aesthetic implications of his language were quirky, colourful, whimsical or unintentional. They are a fundamental feature of his theory. It would be overreaching, however, to conclude that Darwin's view is exclusively arbitrary and coevolutionary. In various passages, Darwin's conception is clearly consistent with sensory/cognitive bias and quality/condition indication as possible advantages to choice. But it is also clear that Darwin's theory was not synonymous with the modern good genes or direct benefits mechanisms either. Darwin's model clearly included the possibility of the evolution of arbitrary traits that provide no naturally selected, direct or indirect benefit to the female. Thus, a contemporary, Darwinian theory of sexual selection should be cast in a similarly broad fashion to incorporate the possibility of both arbitrary traits and traits that provide additional adaptive advantages to choosers.

Criticisms of Darwin's proposal of sexual selection by mate choice were swift, broad and successful, ultimately leading to the nearly complete abandonment of the theory of sexual selection by mate choice for a century.[1] The singular productive exception in the following century was the revolutionary, but rudimentary, verbal model of Fisher [8–10], which made little impact at the time. After imagining the origin of mating preference through natural selection, Fisher observed that genetic variation for mate preference would become correlated with genetic variation in display traits merely by the action of mating preferences alone. He predicted the result would be the evolution of a display trait that

> owes nothing to natural selection, which may even have turned against it, but it still increases in splendour and perfection, and the importance attached to it by the opposite sex still increases, so long as it retains a balance of advantage. [8, p. 187]

In his comparison of display traits to the 'points' of perfection used by ornamental bird breeders and agronomists, Fisher's verbal model picked up precisely where Darwin's aesthetic theory left off decades before. Fisher sketched out a genetic mechanism for the evolution of mating preferences for display traits that are merely attractive and evolved without any additional benefit to preference. In this way, Fisher's model lays the groundwork for a genetic theory of Darwinian aesthetics. Of course, by the time sexual selection was revitalized in the 1970s and 1980s, the critical, aesthetic component of Darwin's mate choice theory was completely missing. Mathematical models by Lande [5] and Kirkpatrick [6] fully achieved the aesthetic sexual selection mechanism envisioned by Darwin and Fisher, but these models were driven to the margins of the field by the untested belief in the universality of natural selection on mating preferences [4,7,17].

3. WALLACE'S ANTI-AESTHETIC CRITIQUE

Of all of the critics of Darwin's theory of sexual selection by mate choice, A. R. Wallace was the most effective. Wallace's critical view of mate choice grew gradually in strength after his first review of *Descent of man*, and was complete by the late 1880s and 1890s [18]. Today, Wallace's views have largely been laundered of any relevance to contemporary research because we have focused on his wackier ideas. But this view is not entirely accurate [12]. Wallace did expend a lot of energy describing why sexual selection by mate choice should not happen frequently. He argued that sexual dimorphism was the result of natural selection against brilliant females, not selection for brilliant males. He argued that, like the brilliant colours of our spleen, liver and other internal organs, many conspicuous features of male phenotypes were merely accidental by-products of vigorous organismal function. Likewise, he argued that courtship displays were incidental, external expressions of the inner physiological vigour and exuberance of maleness, like a nervous tic. These creative but highly questionable arguments went on for pages, and largely determine modern views of Wallace's opinions. But, as Helena Cronin [12, p. 123] documents in her excellent history of the Darwin–Wallace sexual selection debate, *The ant and the peacock*, Wallace never fully denied the possibility of evolution by mate choice. Most of his arguments merely advocated against its likelihood. However, the most relevant and forceful aspect of his critique came from his statements about what would happen when mate choice *did* occur. Here, Wallace [18, pp. 378–379] explicitly stated:

> The only way in which we can account for the observed facts is by supposing that colour and ornament are strictly correlated with health, vigor, and general fitness to survive.

Suddenly, to modern ears, Wallace's opinions do not sound so half-baked! Wallace's view is entirely consistent with orthodox opinion today. This statement would be entirely at home in any modern biology textbook, or the introduction to practically any contemporary paper on intersexual signalling. Indeed, it is likely to capture the opinions of the majority of the readers of this paper.

It may come as a shock to contemporary biologists to learn that the man who is largely credited with killing intersexual selection theory for a century was actually the first person to clearly articulate the fundamental premise upon which almost all current sexual selection research is based. But this irony reveals something fundamental about intellectual structure of contemporary sexual selection theory. It should be clear as well that Wallace's statement was stridently anti-Darwinian. As Cronin [12, p. 190] states of Darwin and Wallace, 'when it came to the question of why females choose the mates they do, the two of them were poles apart'.

How did this happen? What about Wallace's opinion (and therefore most congruent contemporary views) was so anti-Darwinian? An important component of the answer lies in understanding that Wallace's defeat of evolution by mate choice was partially semantic. Having conceded that evolution by mate choice *could* occur, but only in a special way that is entirely consistent with modern theory, Wallace called the evolutionary mechanism by which females choose mates whose displays were correlated with health, vigour and fitness to survive *natural selection*, not sexual selection. In this same section of *Natural selection and tropical nature* which was headed 'Natural selection as neutralising sexual selection', Wallace wrote:

> ...if there is (as I maintain) such a correlation [between ornament and health, vigor and fitness to survive], then the sexual selection of color or ornament, for which there is little or no evidence, becomes needless, because natural selection, which is the admitted *vera causa*, will itself produce all the results... Sexual selection becomes as unnecessary as it would certainly be ineffective. [18, pp. 378–379]

If Wallace refers to mate choice for ornamental traits that indicate health, vigour and fitness as natural selection, what was Wallace referring to as 'sexual selection' in this passage? Having invented a thoroughly modern view of evolution by mate choice and calling it natural selection, what was left of Darwin's theory for Wallace to adamantly reject? For what 'needless', 'unnecessary' and 'ineffective' evolutionary mechanism was there 'little or no evidence'? What force was being 'neutralised' by natural selection?

Wallace was referring, of course, to Darwin's fully aesthetic view of sexual selection as a 'taste for the beautiful'. Wallace was arguing against the possibility of any arbitrary, uncontrolled, unregulated and potentially decadent consequences of female mate choice that were outside the control by natural selection. Wallace justified this conclusion with the strikingly modern statement that, 'Natural selection acts perpetually and on an enormous scale'. Nearly identical edicts are used in contemporary papers to defend the untested assumption that mating preferences are under ubiquitous natural selection. These contemporary statements accomplish the same Wallacean goal—to reject the possibility of arbitrary sexual selection process.

What readers took away from Wallace's critique was that sexual selection was not very likely, and even if it did occur, it would be entirely 'neutralised' by, and therefore identical to, natural selection. Thus, biological research programmes could proceed confidently to study natural selection exclusively. Mate choice had no independent effects, and so the entire concept could be safely abandoned.

Almost a century later, Wallace's quality correlation idea was reinvented by Amotz Zahavi, apparently without the awareness of Wallace's quite explicit proposal. However, the second time around the same mechanism was defined as sexual selection instead of natural selection. Zahavi [19; p. 205] wrote that 'Wallace... dismissed altogether the theory of sexual selection by mate preference', but his statement pages later is entirely consistent with Wallace's [18, pp. 378–379] proposal:

> I suggest that sexual selection is effective because it improves the ability of the selecting sex to detect quality in the selected sex. [19, p. 207]

The semantic tension over the boundary between natural and sexual selection lives on in the contemporary debate over the definition of sexual selection.

Darwin referred to sexual selection as occurring through variations in opportunity to mate (which reasonably includes fertilization and appropriately captures post-copulatory female preference). This definition was followed in much modern theory [20–23]. Recently, however, Fuller *et al.* [24], Kokko *et al.* [25,26] and others have recast the definition of sexual selection to include the variation in the *quality* of the mates acquired. Regardless of whether this has been done for the convenience of mathematical modelling or for a broader intellectual purpose, the result is a semantically new way of accomplishing Wallace's original goal—to neutralize the possibility of any evolutionary consequences of sexual selection that are independent of natural selection. Most natural selection on preferences is redefined as sexual selection. Any independent consequences of mate choice have been defined out of existence.

I cannot review the large topic of the definition of sexual selection by mate choice here, but it should be clear that this is not a semantically neutral issue. As Wallace demonstrated in his Victorian era victory over sexual selection, the definitions of natural and sexual selection affect how we think biotic nature evolves. Whether we are even permitted to imagine that mate choice may give rise to arbitrary traits through trait-preference coevolution will ultimately depend on how these mechanisms are defined. Most importantly, it would be hard to claim that any theory in which natural selection and sexual selection are synonymous, or obfuscated, could be considered Darwinian.

Advocates of good genes and direct benefit mechanisms of sexual selection who would reject this association with A. R. Wallace might be surprised to find that others of their number do not. Richard Dawkins [13] has eagerly embraced Cronin's [12] 'Neo-Wallacean' label, and described the discoveries of Zahavi [19], Hamilton [27] and Grafen [17] as 'sophisticated Neo-Wallacean' triumphs over Darwinian vagueness. Dawkins [13, pp. 265–266] writes:

> For Darwin, the preferences that drove sexual selection were taken for granted– given. Men just prefer smooth women, and that's that. Alfred Russel Wallace, the co-discoverer of natural selection, hated the arbitrariness of Darwinian sexual selection. He wanted females to choose males not by whim but on merit…
>
> For Darwin, peahens choose peacocks simply because, in their eyes, they are pretty. Fisher's later mathematics put that Darwinian theory on a sounder mathematical footing. For Wallaceans, peahens choose peacocks not because they are pretty but because their bright feathers are a token of their underlying health and fitness … Darwin did not try to explain female preference, but was content to postulate it to explain male appearance. Wallaceans seek evolutionary explanations of the preferences themselves.

Instead of taking Darwin's aesthetic language as a hypothesis about the mechanism of evolutionary elaboration of traits and preferences, Dawkins confounds the arbitrariness of Darwinian traits with a perceived ambiguity about Darwin's evolutionary mechanism. The anti-aesthetic, anti-arbitrary, Neo-Wallaceans are portrayed as scientifically progressive, while aesthetic views of Darwin are portrayed as fuzzy and incomplete. Dawkins admits Fisher's more solid theoretical grounding for the arbitrary, but fails to entertain any modern Darwinian/Fisherian alternative to the Wallacean solution. Dawkins further confounds the question of the origin of preferences with the evolutionary elaboration of traits and preferences (see §5*c*, *Red Herrings*).

Even those who reject the Wallacean origin of the core concepts within contemporary sexual selection theory will likely sympathize with Wallace that the purely aesthetic elements of Darwin's theory—aesthetic faculties and the taste for the arbitrarily beautiful—have little place in evolutionary biology.

4. AESTHETIC EVOLUTION

There is no reason to propose a new theory, model or term in science, or to revive an abandoned one (even a Darwinian one), unless it does some useful intellectual work: that is, unless it provides the opportunity to change the way we do science, the way we think and how science proceeds. So it is important to ask, 'Can the concept of the aesthetic do any useful work in evolutionary biology?' I think so, but building a concept of aesthetic evolution that is heuristic and intellectually productive requires some more background.

Fundamental to an aesthetic evolutionary process is the recognition of the distinction between those components of the phenotype that function primarily in the physical world and those that function through perception by other individuals. For example, the roots of a plant function in absorbing water and nutrients from the soil, and stabilizing the plant in its substrate. The functions of a root can be described entirely by physical and physiological data. In contrast, the flower is an advertisement by the plant to animal pollinators that provides a physical structure to mediate the exchange of nectar for pollination transport services. Parts of the flower function in the production and positioning of ovules and pollen for sexual reproduction, but the conspicuous components of the flower—including fragrance, and the number, shape and colour of petals and sepals, etc.—function in communicating to and attracting animal pollinators. Unlike roots, these components of the flower function through the perceptions of them by the nervous systems of other organisms, and not merely in the physical world. An animal must regard the flower, evaluate that experience and then decide whether to feed on its nectar, or to reject it and proceed to evaluate another competing floral nectar source. (Although the neural events in the brain of the pollinator during sensory evaluation and choice are physical events, they are not yet reducible to any description of these physical events.)

As a consequence of cognitive evaluations and foraging decisions, pollinators will either aid the plant in achieving pollination or not, and thus determine the reproductive success of the plant. Unlike the root, a complete description of the functions of a flower requires understanding of the sensory experiences and subsequent cognitive states of the populations of organisms observing that flower and their consequent evaluations and foraging decisions based on this sensory input. A successful floral design is not determined by adaptation to mere physical challenges, but by the frequency distribution of sensory evaluations, consequent cognitive states, and economic decisions of a dynamically evolving population of potential pollinators living within a diverse community of competing floral species. Thus, it is not an accident that flowers are traditional examples of aesthetic beauty in nature, and roots are not. Flowers have a neural/cognitive functional substrate that roots entirely lack.

Like animal pollinated flowers, intersexual display traits are also examples of components of the phenotype whose function cannot be understood without a description of the consequent neural/cognitive states of a population of other individuals—potential conspecific mates. Intersexual display traits exist physically and are subject to physical constraints. Their communication functions are mediated by the physical world through acoustic, optical, chemical and even electrical mechanisms. But intersexual traits *function* through the perceptual evaluations of other individuals. Critically, the success of any intersexual trait is determined by the frequency distribution of the sensory/cognitive preferences in the population of prospective mates and by their probability of mating encounters. Intersexual display traits do not ‘do’ anything in the physical world alone. Rather, they function in perceptual worlds—the *Umwelt*—of potential mates.

A second critical feature of aesthetic evolution is that it requires *sensory evaluation* of the input acquired by the receiver. Here, evaluation means not merely cognitive distinction of the signal from background noise, or from other communication signals in a repertoire, or decision-making in general, but the specific cognitive comparison of the signal to an innate template, to other instances of the same signal perceived simultaneously from another signaller or to memories of previously observed signals (i.e. some cognitive distribution function of signal variation acquired through previous interactions), or a combination of these. Evaluation results in the expression of a preference or choice—either a positive association with the signaller, rejection of the signaller or refraining from making a choice.

I consider evaluation to be distinct from trait ‘assessment’, which has been defined as a cognitive analysis of adaptive information encoded by the trait [28]. Defining mate choice as involving the efficient acquisition of information [28] assumes that mate preferences are under natural selection to encode information of direct benefits or good genes. Arbitrary mate choice has again been defined out of existence. Like many aspects of current sexual selection theory, this view of mate choice has developed in an intellectual environment in which natural selection on preferences is assumed. Yet, this assumption should be subject to scientific testing, and not built into the language and theory of the discipline. In contrast, evaluation is a neural process that may or may not include processing of any encoded information beyond the stimulus itself. Evaluation includes the opportunity that the trait is merely preferred, and communicates no additional information.

For example, the perception by a bird of a conspecific alarm call is not subject to evaluation, because individuals who wait to respond only to those alarm calls they prefer are likely to suffer fitness consequences by ignoring an alarm. Classic work shows that avian alarm calls may be differentiated in response to aerial or terrestrial threats [29], but recognition of conspecific types of alarm calls is not evaluation, as I propose it, because birds do not show a preference in response to variation in alarms. They do not fly off just in response to the prettier, or more alluring, alarm calls. In contrast, perception by a female bird of a courtship song in the appropriate season is likely to be subject to evaluation, which contributes to mate choice. This evaluation may be made entirely on the basis of the cognitive reaction to the stimulus itself, in the absence of any encoded information about quality or condition. (Of course, alarm calls could be assessed with respect to their veracity, but that would involve calling a bluff of the signaller by independently assessing the risk of threats following a series of alarm calls, and potentially ignoring the future alarm calls of a liar because of their inaccuracy, rather than because of their form, sensory composition or content.) As with flowers and roots, it is not an accident that bird songs (which are subject to evaluation) are frequently referred to as beautiful, but alarm calls are not.

Although it may not be required, I will assert here that the concept of the aesthetic evolution may be productively restricted to include only instances of the coevolution of the signal and its evaluation. This restriction would require that the concept of aesthetic evolution does the additional intellectual work of distinguishing aesthetic evolution from the simplest cases of pleiotropic natural selection on mating preferences, or on the sensory system, such as sensory bias. The pre-existing bias mechanism of mate choice proposes that display traits that conform to pre-existing sensory and cognitive biases will evolve [28,30]. Sensory biases are proposed to evolve by prior natural selection on the neural systems for other functions outside mate choice. Such natural selection could have arbitrary, pleiotropic effects on mate choice (see §5*b*). Requiring aesthetic evolution to be coevolutionary would eliminate these simplest cases of sensory bias and ensure that the concept of aesthetic evolution describes more than merely pleiotropic effects of natural selection on the sensory system.

A coevolutionary requirement to aesthetic evolution, however, would not eliminate most instances of evolution by good genes or direct benefits evolution. Although these sexual mechanisms do not assume or require coevolution of traits and preferences, they are entirely compatible with it. Given that display traits and mating preferences have not evolved independently in each species and population, the fact that traits and preferences are phylogenetically ‘coupled’ [28,31] is abundant evidence of trait/preference coevolution (see §5*c*).

In summary, aesthetic evolution requires: (i) a component of the phenotype that functions as a signal through perception by another individual, and (ii) sensory/cognitive evaluation of those perceptions by the receiver leading to the exercise of preference/choice. The action of preference leads to differential success among signals, leading to aesthetic evolution. Aesthetic evolution could be further restricted to require: (iii) the coevolution of the signal and its evaluation. Put simply, aesthetic evolution is an emergent property of choice based on sensory and cognitive evaluation of a signal, and reaches its greatest complexity through the coevolution of a signal and its evaluation. Accordingly, there are a few phenomena, in addition to intersexual selection, that plausibly meet these criteria, including flower/pollinator interactions, fruit/frugivore interactions, some aposematic signalling, offspring begging, and various forms of mimicry. These have all been classic topics in evolutionary biology. Indeed, after publishing the *Origin*, Darwin wrote several books and articles about floral/pollinator coevolution during the same decades in which he worked on sexual selection [32,33].

Aesthetic evolution, as defined here, would include many examples of good genes and direct benefits processes. For example, as natural selection on preferences varies among environments, traits and preferences will coevolve and codiversify. Thus, aesthetic evolution can include utilitarian traits that evolve by good genes or direct benefits mechanisms. (After all if the Guggenheim Museum of Art can mount an exhibition of motorcycles, then the aesthetic can include the utilitarian as well.) However, the good genes or direct benefits mechanisms do not include all examples of aesthetic evolution.

This concept of aesthetic evolution will require us to reconsider some of the broader structural features of the discipline of sexual selection. The dominant role of natural selection on preferences has been so rarely questioned that much of the vocabulary of the field has incorporated it implicitly (as in the discussion of evaluation versus assessment above). For example, secondary sexual signals are frequently characterized as being composed of signal content and signal design [28]. It has been assumed that signal content encompasses information about signaller quality or condition that is advantageous for the chooser to know, and that signal design provides efficiency to communication of signal content, assuming that individuals are under natural selection to make mate choices efficiently [28]. Although both of these processes are plausible, we cannot merely assume that preferences are under natural selection for adaptive information and efficiency, and then define terms in the field around that assumption. Indeed, it is entirely possible that a signal's content *is* its design, and that it evolves merely because it is arbitrarily attractive to mating preferences. Likewise, the assumption of natural selection on mating preferences has led many to interpret any possible cost of mate choice—e.g. temporal and energetic tradeoffs due to mate searching, predation risks, etc.—as evidence of *differential costs* which are necessary for selection to take place (see §5*d*). But these hypotheses need to be tested, not assumed. Nor should adaptive assumptions be built into the definitions and intellectual structures of the discipline. Recognition of Darwinian aesthetic evolution will require reorientation of much of the current theoretical framework which is based on the untested hypothesis of natural selection on preferences.

So does the concept of aesthetic evolution do any useful intellectual work in science? I think so. Most importantly, recognizing aesthetic evolution will help us distinguish whether evaluative evolution in general, and the coevolution of a signal and its evaluation specifically, gives rise to distinct evolutionary patterns and consequences. There is every reason to think that it does. For example, the entirely physical challenge of cracking open a seed with a bird beak has a finite set of physical solutions. Consequently, we see a limited set of convergent finch-like beaks among the many avian lineages that have evolved a granivorous diet. However, the primary function of many male bird songs is to succeed at the problem of attracting a mate, and success in a functional substrate composed of a dynamic population of cognitive preferences is a much more open, less deterministic, more complex challenge. Being attractive to a population of conspecific 'minds' is a much less constrained problem, with a broader, potentially infinite set of possible, frequency-dependent solutions. Selection on phenotype to succeed within a selective landscape composed only of neural or cognitive evaluations and preferences will result in more variable set of solutions than natural selection by external environmental factors, or even other sensory factors (e.g. alarm calls versus songs; flowers versus roots). The empirical challenge of the study of aesthetic evolution will be to establish whether and how coevolution through perceptual evaluation and the exhibition of preferences contributes to any distinct patterns, mechanisms or modes of evolutionary change.

Of course, natural selection can be very dynamic and frequency dependent; likewise, neural and cognitive evaluation may be subject to intrinsic physical or developmental constraints or sensory biases, including at the broadest level the existence of a limited number of sensory systems. Identifying the process of aesthetic evolution will allow us to recognize what patterns, tempos and modes of evolutionary change result from selection by external/physical or neural/evaluative substrates.

More broadly, just as Darwin's revolutionary aesthetic views were threatening to Wallace's Victorian adaptationism, the recognition of the breadth of aesthetic evolutionary process will challenge the contemporary view that natural selection is solely responsible for the origin of form and design in the biotic world. This was clearly not Darwin's view. Rather, he proposed sexual selection by mate choice as a novel solution to what he perceived as a major limitation of his theory of natural selection—the failure to adequately explain the evolution of beauty in nature. Most researchers have become convinced that the Neo-Wallacean theory of sexual selection including natural selection on preferences provides a sufficient explanation of beauty in nature, and that the Darwin–Wallace debate is over. The debate, however, is not over because the current paradigm rests on an untested assumption of the ubiquity of natural selection on mate preferences. Recognizing aesthetic evolutionary process will revive the Darwin–Wallace debate over the potential limits of natural selection in the modern context.

5. AESTHETIC EVOLUTION AND LANDE–KIRKPATRICK NULL MODEL

(a) *Darwin and the Lande–Kirkpatrick null*

To resolve the Darwin–Wallace debate, we must pursue research in which arbitrary sexual selection is fully functioning in the discipline, and not merely a historical footnote. The intellectual path to such a framework runs directly from Darwin [11], to Fisher [8–10], to Lande [5] and Kirkpatrick [6], to Kirkpatrick & Ryan [7], to the LK null model [4]. Darwin's theory of sexual selection is too broad, ambitious and embryonic to be equated with the LK null alone. But the LK null is clearly required to capture the full dynamics of the process that Darwin proposed. In contrast, the untested belief in universal natural selection on preferences is a Neo-Wallacean view that leads to a rejection of any role for null models in sexual selection.

The critical issue is whether intersexual selection has any independent evolutionary consequences beyond those of natural selection alone. Answering this question requires entertaining the possibility that mating preferences are *not always* under natural selection. Entertaining the possibility of limits to adaptation is a fundamental feature of what makes evolutionary biology a science. That is, the assumption of natural selection on mating preference must be tested against a null hypothesis. These conditions describe the LK null model, which assumes genetic variation in trait and preference and no natural selection on preference [4].

A heuristic, legitimately Darwinian, contemporary theory of intersexual selection theory would: (i) fully incorporate the LK null model of trait and preference evolution, (ii) test for pre-existing biases, *and* (iii) invoke the various sources of natural selection on mating preferences only once the LK null and sensory bias have been falsified.

The LK null is essentially the Hardy–Weinberg of intersexual selection [4]. Like Hardy–Weinberg, it emerges as a mathematical consequence of genetic variation alone; it is the description of the evolutionary consequences of the existence of genetic variation itself. Of course, it describes a very special case of genetic variation selecting on other genetic variation in the same population. This interesting feature is exactly why Fisher [8–10] was intrigued by the idea, which was first published in 1915—only 8 years after Hardy–Weinberg.

Good genes and direct benefits mechanisms all require additional natural selection on mating preferences to occur (or the equivalent process redefined as a form of sexual selection itself). Thus, the LK null is equivalent to all these models with the parameter value for natural selection on mating preferences as zero [4]. The dynamics of the LK null model are changed only quantitatively, not qualitatively, by the existence of natural selection on display traits themselves [5,6].[2] Given that the fundamental issue in sexual selection is the explanation of the evolution of mating preferences and not display traits [7], natural selection on display traits can appropriately be incorporated in the LK null [4].

The potential for an LK null process lies in wait within of any population under intersexual selection in the presence of genetic variation. Natural selection on preferences for honest quality/condition indicating traits will always be susceptible to the erosion of the trait/quality/condition correlation by mutations for male cheating. Fisher viewed the unhinging of an indicator trait from its quality information as an obvious consequence of the evolution of female preference. Yet, even the possibility of this occurrence is rarely considered in modern research [4]. Despite the paradigm of promiscuous, cheating, male selfishness at the heart of reproductive behavioural ecology, current sexual selection research rarely entertains the possibility that selfish, cheating mutations can erode the trait/quality correlation. (Perhaps the one paradigm more powerful that the concept of the promiscuous, cheating, selfish male is the idea that natural selection is the sole source of form and design in the biotic world. To protect the beautiful idea of encoded meaning in ornamental traits, must we forget about the Selfish Gene?) One modern solution to this conundrum (in addition to ignoring it) has been to propose that honest indication traits evolve to be particularly robust to encoding the rapidly evolving features that constitute male viability [27]. However, precisely because of this quality, robust indicating traits would also be highly constrained from further evolving, contradicting the evolutionary pattern of exorbitant diversity that sexual selection was devised to explain [2].

(b) *Sensory/cognitive biases and the null*

Some researchers who are uncomfortable with the LK null remain comfortable with the concept of pre-existing sensory or cognitive biases. (For convenience, I will use the term 'sensory bias', but this concept should include similar cognitive biases as well [34].) They may prefer to view all potentially arbitrary components of display traits as due to sensory bias. Perhaps this is because sensory bias has had a more active presence in the literature over the past 20 years than the LK mechanism [28,30], but it is more likely that many evolutionary biologists are more comfortable with the idea that natural selection has shaped these sensory biases pleiotropically, and therefore natural selection is still responsible, at least indirectly, for the form of such arbitrary traits. In this conception, the evolution of arbitrary display traits is the unexpected but explicable consequence of natural selection, rather than the intrinsic result of an inexplicable, non-adaptive evolutionary process (i.e. the LK null).

Sensory/cognitive bias is simultaneously a very simple idea and a surprisingly difficult concept to circumscribe. Sensory bias is not a hypothesis about preference evolution. At its most succinct, the pre-existing sensory/cognitive bias hypothesis states that display traits will evolve if they correspond to pre-existing preferences [7,28,30]. Pre-existing mating preferences are hypothesized to evolve through prior mechanisms that are unrelated to mate choice—usually as a pleiotropic effect of natural selection on the function of sensory and cognitive systems. When hypothesized in isolation from all other evolutionary forces (i.e. under conditions when the hypothesis is easiest to test), sensory bias becomes a hypothesis about the order of trait preference evolution—preference evolves *before* traits, and traits evolve in response to pre-existing preferences. This process will yield traits that are arbitrary and communicate no information, but the process may also yield traits that are non-randomly related to the sensory environment—i.e. traits that are more efficient to perceive sensorally because sensory systems have evolved to be very efficient in that specific sensory environment [28]. This restricted class of pre-existing bias hypotheses—preferences before traits—can be tested with comparative phylogenetic analyses of the distribution of traits and preferences [28,30,31].

The real complexity is that pre-existing sensory/cognitive biases are not limited to the strict context in which they are more easily tested, but are a simultaneous component of any mechanism of preference evolution. For example, imagine a population with a male display trait and a female mating preference for that trait that is evolving by the LK null, good genes *or* direct benefits mechanisms. Over time, imagine that the population evolves to include new variation in the trait value that, for unrelated prior physiological, neurological or cognitive reasons, is subject to some additional behavioural response (either preference or aversion). This behavioural response has never been uncovered or exposed before by evolution because there has never been an opportunity; mate choice and this intrinsic feature of the sensory or cognitive systems have never been juxtaposed before. Such an inherent, pre-existing sensory response would constrain or bias the evolution of trait and preference in the population. Viewed from this perspective, sensory bias is not a separate sexual selection mechanism, but an omnipresent possibility that is a component of any evolutionary mechanism of intersexual selection.

By analogy, this broad concept of sensory/cognitive bias can be conceived of as a pre-existing landscape of intrinsic behavioural responses to potential social, sensory stimuli. Some variations in the landscape may be due to prior sensory evolution for efficient sensory perception in the sensory environment. Others may be due to neural mechanisms of pattern detection or analysis that are a consequence of the structure and development of sensory systems or the brain. As populations evolve over the landscape through changes in display phenotype through whatever mechanism—adaptive or arbitrary—they may expose prior sensory biases that will influence the course of evolutionary change. Further, the landscape of biases itself can evolve pleiotropically as sensory and cognitive systems evolve in response to ecological or environmental change [28]. The possibility of such a dynamic process demonstrates an important limitation to the term 'pre-existing' biases to capture this concept. In the field of evo-devo, we have learned that the mechanisms controlling how organisms develop and grow place constraints and biases on how they can evolve and how anatomical novelties originate. In a similar way, the underlying landscape of sensory biases creates differential possibilities that have a similarly structural origin, but have a special impact because of their role in the evolution of intraspecific communication.

This broad concept of sensory bias is extremely difficult to test, which is why most research in the area has focused on testing the strict sensory bias hypotheses phylogenetically. But just because a hypothesis is difficult to test does not mean that it is not a relevant and important component of trait and preference evolution. Just as physical constraints can never be evaded (organisms do live in a physical world), sensory bias can never be completely irrelevant because communication occurs through sensory systems.

Although omnipresent, however, the broad concept of sensory bias by itself still has limited power to explain trait and preference differentiation *among* species without reason to hypothesize correlated evolutionary radiation of the sensory/cognitive bias 'landscape' among these species. This prospect runs exactly counter to the conserved mode of bias evolution that would allow the strict sensory bias hypotheses to be testable phylogenetically [28,30,31]. Although it is a purely empirical question that remains to be answered, sensory bias seems to me unlikely to explain the bulk of secondary sexual trait *and* preference radiation in groups of closely related species.

In conclusion, sensory bias is a consistent component of the evolution of traits and preferences through any mechanism, but since it is not itself a hypothesis about the evolution of preferences, sensory bias has limited power to explain the evolution of trait *and* preference diversity. Therefore, it is not an adequate null hypothesis for the evolution of traits *and* preferences. Sensory bias is 'in the water', and cannot be avoided, but it cannot itself provide a functional null model for the evolution of the observed variations in traits and preferences. What sensory bias and the LK null model share is a focus on the evolutionary consequences of mate choice in the absence of natural selection for specific variations in mating preference.

I proposed the LK mechanism as the null model of the evolution of trait *and* preference by sexual selection [4]. Since sensory bias is not a mechanism for the evolution of preferences, the LK mechanism is the preferred null model for intersexual selection. Of course, if there is no heritable variation for mating preference (as in strict sensory bias models), then the LK mechanism is not an appropriate null model of sexual selection under these circumstances.

(c) *Red herrings*

The historical antagonism to arbitrary sexual selection mechanisms [17] may have contributed to mistaken impressions of what the LK null model predicts. Consequently, it is appropriate to discuss a few 'red herrings', or misleading notions about what the arbitrary sexual selection predicts, and what constitutes evidence of natural selection on preferences.

First, it is observed that the LK null does not explain the origin of preferences, but assumes them. This is absolutely true. Dawkins aims the same critique at Darwin (see §3). However, this issue is completely irrelevant to most species. Most investigations of reproductive behavioural ecology are not required to explain the origin of sex. Why? Because the origin of sexual reproduction is known to have occurred before the evolution of the species being studied. The origin of sex is a fascinating and important question, but it is recognized to be a distinct subject from reproductive investment, parental care, sexual selection, etc., which encompass most of reproductive behavioural ecology. Research on the origin of sex requires special experiments and species to address its questions effectively. Few instances of sex are specifically relevant to testing the evolutionary origin of sex. Likewise, the origins of mating preference are very ancient relative to most species in which sexual selection is being studied. For example, the origin of mating preferences in birds probably occurred prior to the breakup of Gondwanaland [4]. Thus, the issue of the origin of mating preference is irrelevant to the study of sexual selection in birds today. The potential role of natural selection in the origin of mating preferences is a fascinating topic that probably has nothing to do with any living birds at all. The same conclusion applies to most other species in which sexual selection is being studied.

A related claim is that there is little evidence of the genetic covariation and coevolution that the LK null predicts. There are a lot of reasons why the LK mechanism might still be active, but the conditions for detecting such genetic correlations might be rare [4]. From a comparative perspective, however, it is obvious that coevolution in traits and preferences is virtually ubiquitous. Because mating preferences have not evolved uniquely in every species but originated in some prior ancestors, the observation that the vast majority of species that exhibit mate choice show clear mating preferences for their own species is *prima facie* evidence of trait and preference coevolution. Thus, the evidence of the coevolution of trait and preference is immense, and not restricted to experimental demonstration of genetic correlation of traits and preferences within a population.

More recently, it has been claimed that the Fisher process (i.e. LK null), in which preferences evolve only through the indirect benefit of sexually attractive offspring, is continuous with, and therefore indistinguishable from, the good genes mechanism in which preferences evolve through the indirect benefit of fitter male and female offspring [25,26]. Kokko *et al.* [25,26] have further claimed that the distinction between arbitrary and good genes traits has never been made satisfactorily. They wrote,

> We therefore conclude that distinguishing between preferences for 'arbitrary' and 'non-arbitrary' male traits is, in itself, arbitrary. [26, p. 1337]

This is incorrect. The difference between them actually is quite profound [4], and has been the direct cause of the animosity towards even the possibility of arbitrary aesthetic trait/preference evolution for over a century from Wallace [18] to Grafen [17]. The distinction lies at the heart of the Darwin–Wallace debate, and was a substantial reason why Darwin proposed the mechanism of mate choice by sexual selection as an independent evolutionary mechanism distinct from natural selection. To reiterate, an arbitrary trait merely corresponds to a mating preference that selected for it [4]. Arbitrary does not mean random, ahistorical, accidental or unfathomable. Arbitrary means that a signal communicates no additional information other than its availability for evaluation and its potential to correspond to a mating preference. An arbitrary trait is neither honest nor dishonest because it does not communicate any information that can be untruthful. It just exists.

Of course, if there is some indirect benefit to preference from good genes simultaneously with indirect selection on preference through its genetic correlation with the trait, then these mechanisms will be difficult to distinguish empirically [25,26]. But this empirical challenge is not a reason to obfuscate the conceptual difference between the two mechanisms, because the predictions they make about the nature of signal content and design in organisms are fundamentally different.

(d) *How to reject the Lande–Kirkpatrick null*

I have received criticisms of the LK null as too variable, predicting everything, or even nihilistic. Of course, evolutionary biologists who assume the universal importance of natural selection in their work may be understandably disturbed to learn that diverse radiations of complex, highly structured secondary sexual trait designs can evolve entirely without the input of natural selection. Darwin, too, was eager to communicate this message. Evolutionary biologists must face the possibility of the complex consequences of genetic variation selecting upon other genetic variation through sensory evaluation alone, and proceed to establish whether this process is common in nature.

Falsifying the LK null will not be easy. The core prediction that distinguishes good genes and direct benefit models from the LK null is the presence of natural selection on preferences. Thus, critical tests would consist of measuring gradients of natural selection on mating preferences. Ultimately, it would be important to distinguish whether natural selection on preferences occurs through good genes or direct benefits mechanisms (including natural selection for preferences for traits that increase mate choice efficiency), or is a pleiotropic effect of natural selection on some other aspect of phenotype (constituting a preference bias). Do females within a population that vary in mating preferences vary in viability and fitness (direct benefits)? Do females that vary in preference receive indirect fitness benefits exclusively through their son's sexual advantages (LK null) or through increased viability of both their sons *and* their daughters (good genes)? These are the core issues that need to be tested.

For example, Gerlach *et al.* [35] recently published an extraordinary dataset with evidence that dark-eyed juncos (*Junco hyemalis*) sired by extra-pair copulations have higher lifetime fitness. In particular, Gerlach *et al.* found that males' extra-pair offspring gain their fitness increases through their own extra-pair offspring, not through increased survival or within-pair fecundity. Although the discussion of the results and the media reports about them were framed entirely in terms of the good genes benefits of extra-pair copulations, the data are actually entirely congruent with an arbitrary LK null mechanism (N. Gerlach & J. McGlothin 2012, personal communication).

Various other types of evidence that are commonly considered to be support for good genes or direct benefits mechanisms are actually explicitly predicted by the LK null model [4]. For example, display trait costs are at the heart of most honest indication mechanisms [36]; so trait costs are frequently measured to establish how a trait is an honest indicator of quality. This entire body of literature, however, has ignored the prediction by the LK null model that arbitrary traits will be far from the natural selected optimum, resulting in substantial production, maintenance and viability costs to arbitrary traits (as both Darwin and Fisher understood). This issue was a big part of Darwin's motivation to propose sexual selection in the first place. As in the LK null, Darwin saw the viability costs of ornament as trading off with its sexual advantages. Today, consideration of any arbitrary sexual selection process is usually rejected *a priori*, and trait costs are routinely interpreted as direct evidence of the reinforcement of signal honesty. This is incorrect.

Recently, Byers *et al.* [37] and others [38] have proposed that mating preferences for physical displays can evolve through natural selection for display that demonstrates the vigour, energy and performance skill of the prospective mates. Advocates of the 'motor performance hypothesis' have failed to consider the LK null model, which specifically predicts the evolution of extreme preferences for extreme display traits that will consequently require dexterity or skill, and may reach energetic or physiological limits of the displaying individuals. There is no reason to view the extremity of physiological demand or performance skill as evidence of natural selection for the evolution of preferences to assess information about male quality or condition. In short, skill and vigour can be easily incidental consequences of aesthetic extremity, not its cause.

By analogy, the motor performance hypothesis is like proposing that people like classical violin concertos or blues rock guitar because the performers may sweat while playing. Obviously, there are many imaginable musical performances that will cause the performers to sweat to a similar degree that might not be similarly preferred. If we include highly technical atonal violin or guitar music, there would be many performances that would require as much or more skill on the part of the player that would not be similarly preferred. Similar arguments are made for display rate, but these also confuse cause and effect. If a male is sexually unsuccessful at a lek, he may lower his display rate strategically to save energy or to engage in alternative sexual strategies (e.g. display at multiple leks, or pursue females in other contexts). A correlation between display rate, energy expenditure and sexual success does not mean that sexually unsuccessful non-displayers are energy limited or that preferences for display have evolved by natural selection for preferences for quality or condition information inherent in high display rates.

Likewise, evidence of the distinction of display traits from the sensory background is often interpreted as evidence of natural selection on preferences for efficient mate searching and choice [28,39]. However, this literature also ignores the fact that the LK null predicts the evolution of arbitrary traits, which will evolve to be differentiated in any possible sensible dimension. Thus, arbitrary traits are, almost by definition, likely to stand out against the sensory background [4], and these types of analyses have yet to reject the null LK model.

Since Kirkpatrick & Ryan [7], the existence of the costs of mating and mate searching have been universally considered as evidence of natural selection on mating preferences. This is just false. Just because females are exposed to predation risks during mate searching, have limited energy budgets, or risk exposure to sexually transmitted diseases, etc., does not mean that variation in mating preferences will be correlated in any way with avoiding or minimizing any of these costs. The existence of costs of mating is not evidence of differential cost of variations in mating preferences, which are absolutely required for natural selection on mating preferences to occur. We will all die someday (i.e. viability is not infinite), but that fact itself does not mean that we are under natural selection. To demonstrate natural selection on mating preferences, one has to show that natural variations in preference have consequences for the viability of the female, the number of her offspring or their viability. Natural selection cannot be merely assumed to exist.

In summary, research programmes in Darwinian aesthetic evolution require incorporation of the LK null model, which will require testing the assumption of natural selection on preferences.

6. REVIVING THE DARWIN–WALLACE DEBATE

The central question of the Darwin–Wallace debate on sexual selection remains a fundamental issue in evolutionary biology today—Is natural selection the sole mechanism for the evolution of form and design in biotic nature? A trivial solution to the question would be to define all possible forms of sexual selection as types of natural selection, and answer affirmatively. However, the historical animosity to arbitrary sexual selection mechanisms demonstrates that this semantic solution is not really sufficient. It is the mere possibility of the evolution of arbitrary traits and preferences, the mere possibility that this paradigm could be questioned, that is really the problem.

Although the 'adaptationist programme' was critiqued successfully by Gould & Lewontin [40] several decades ago, many researchers in sexual selection appear 'not to have gotten the memo' (G. Rosenthal 2012, personal communication). Because Gould & Lewontin's critique predated the rise of adaptive sexual selection theory and did not focus on mate choice, sexual selection research may have somehow evaded responding to these issues. In short, some aspects of the adaptationist programme remain alive and well in behavioural ecology—especially the untested assumption of natural selection on preferences.

Why is it that so many researchers in sexual selection react so adamantly to the possibility of arbitrary display traits and mating preferences? I think the answer requires a sociological as well as a scientific account [41]. Like Wallace, many contemporary evolutionary biologists *believe* that natural selection is the sole source of form and design in biotic nature, and they hold this principle to be the very cornerstone of our discipline. They have dedicated their professional lives to maintaining, curating, defending and advancing this principle. For many older evolutionary biologists, the formative intellectual event of the 1970s was the 'Hamiltonian Revolution'—the framing of the concept of inclusive fitness and its application to the evolution of social behaviour. The redefinition of altruism as selfishness brought a broad spectrum of previously troublesome sociobiological phenomena under the rational purview of natural selection. Generations to follow were recruited into the discipline with this ethos. Many sought to relive and expand this revolution by redefining secondary sexual ornaments as utilitarian honest indicators of quality or condition [19]. Like Wallace, they used the logic of Darwin's *Origin* to argue against Darwin's *Descent.* Darwin's quaint, Victorian, aesthetic language made this much easier to do. Efforts by Lande and Kirkpatrick to revive genuinely Darwinian theories of arbitrary sexual selection from Fisherian suggestions [5,6] were soon put to rest when Zahavi's initially unworkable idea was made to function theoretically by Grafen [17]. Soon, however, theoretical plausibility came to be seen as logical inevitability.

In 1990, Alan Grafen [17, p. 487] wrote:

> To believe in the Fisher–Lande process as an explanation without abundant proof is methodologically wicked. Such a belief inhibits the search for patterns that might disprove it.

Grafen's claim was rhetorically effective because it demanded proof of the null hypothesis—a logical impossibility. Once the standard of evidence became impossible to meet, it became certain that advocates of Fisherian models would be unable to meet it. This is why there are no recognized examples of arbitrary traits [4]. Ironically, the truth of Grafen's second statement is now exactly reversed. It is the never-tested belief in natural selection on mating preferences that now inhibits the scientific discovery of patterns of trait and preference coevolution that would support a broader, and legitimately Darwinian, model of aesthetic evolution by mate choice.

Grafen [17] further portrayed Zahavi's handicap principle as 'rhyme and reason' and 'an upward struggle from fact'. Of course, in the context of the broader intellectual goal to explain all of evolution by natural selection, 'rhyme and reason' was certain to succeed over a 'methodologically wicked' idea that was 'too clever by half'. In this manner, secondary sexual ornament joined the altruistic among the formerly inexplicable biological phenomenon that had been explained by the rational power of natural selection. Thus, the field accomplished a second, Neo-Wallacean victory over Darwin in almost complete ignorance of the details of the first. Yet the triumph of Zahavian 'rhyme and reason' has been sociological, not empirical. The assumption of natural selection on preferences remains untested, and voluminous evidence that does not confirm the adaptive mate choice paradigm remains unpublished as insignificant results.

Ironically, in today's intellectual environment, Darwin's dangerous idea is not the power of adaptation by natural selection [42]. Darwin's *really* dangerous idea is his own proposal that natural selection fails to explain the evolution of all form and design in biotic nature. Darwin proposed that evolution through aesthetic mating preferences plays an independent role in the evolution of an enormous diversity of secondary sexual traits, including many of the most extraordinary instances of design in nature, such as the ocelli of peacocks (*Pavo*) or male Argus pheasant (*Argusianus argus*). Darwin realized that no other field of biology is so challenging to the generality of the power of adaptation by natural selection as the explanation of the diversity of secondary sexual traits and mating preferences. Darwin bravely faced this intellectual challenge, and he concluded that natural selection was *not* the sole source of form and design in nature. Darwin created an aesthetic theory of mate choice to address the limits of the explanatory power of natural selection. Any modern theory claiming to be Darwinian must do the same.

The field of sexual selection needs to revive the Darwin–Wallace debate. We cannot continue with the current intellectual structure of the discipline, which protects the Neo-Wallacean adaptationist assumptions from being tested and encourages weak confirmation over hypothesis testing. We need to use the generalized tools of scientific inquiry—null models and hypothesis testing.

As in previous debates in evolutionary genetics and community ecology, it is clear that the explicit use of null models will prevail in sexual selection. Ultimately, null models will be adopted by all workers in the field. Accordingly, I look forward to a resolution of the Darwin–Wallace debate in the coming decades. The question is not whether the current paradigm will go down swinging—this is given—but rather, when will the necessary research be undertaken to explore the limits of natural selection to explain form and design in nature? Who will be involved? How will contemporary evolutionary biologists as a whole respond to this explicitly Darwinian challenge to current adaptationist dogma?

Of course, the option is open to continue to oppose the possibility of Darwinian aesthetic evolution, the LK null model or arbitrary mechanisms in sexual selection, but it should be acknowledged that this intellectual position is as anti-Darwinian today as it was when articulated by A. R. Wallace more than a century ago.

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ENDNOTES

[1] Milam [16] criticizes this account, but the evidence she presents documents the conclusion quite well. The many studies of female mate choice during this 'lost' century were all focused on issues other than Darwin's primary concern.

[2] Whether or not an unstable runaway occurs will be influenced by the strength of natural selection on the trait, but a runaway can also occur in the absence of natural selection on the trait. Consequently, I consider that this remains a quantitative and not qualitative difference. Natural selection on the trait *reduces* the conditions under which a runaway can occur, making the LK null more stable.

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