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## Opinion

# Sex-specific assumptions and their importance in models of sexual selection

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Sexual selection is a field coloured by tension and contrasting views. One contested claim is the causal link from the definition of the sexes (anisogamy) to divergent selection on the sexes. Does theory truly engage with this claim? We survey the extent to which theory makes sex-specific assumptions and engages with anisogamy, and discuss these issues in a broader context. The majority of theory in sexual selection makes sex-specific assumptions and does not engage with the definition of the sexes. While this does not invalidate existing results, debates and criticisms regarding sexual selection force us to think deeper about its logical foundations. We discuss ways to strengthen the foundations of sexual selection theory by relaxing central assumptions.

## Disputes in sexual selection theory

Sexual selection is one of the oldest research areas in evolutionary biology [1], and one of the most active today [2], with tension and strongly contrasting views remaining common. These disputes have several inter-related dimensions. One line of debate concerns the binary definition of sexes in evolutionary biology (Box 1), which contrasts with the view of gender as a graded spectrum that has been partially adopted in the biomedical and social sciences [3,4]. Another key point of ongoing contention is the extent to which gender biases have coloured the field of sexual selection and propagated outdated assumptions about sexes and sex roles [5–13]. For example, human societal norms may have contributed to the slow recognition of polyandry in birds, which is now known to be common even in socially monogamous species [14]. Analogous complications can of course influence almost any aspect of evolutionary theory (and science in general), but sexual selection seems to be one of the topics (e.g., alongside social evolution theory [15]) where disagreements and debates appear repeatedly.

We focus here on a related and more concretely quantifiable criticism that concerns one of the central causal claims of sexual selection theory: that the difference in gamete size and number that exists between the two sexes (Box 1) is the cause of divergent selection on mating competition and other sexually selected traits and behaviours. To what extent do typical models in sexual selection theory address this claim? For example, Ah-King claimed that 'the logic is simply missing' in terms of the causal effect of gamete size on mating competition and other sexually selected traits and behaviours [5]. In a critical overview of research in sexual selection, Gowaty [9] argued that the majority of evolutionary hypotheses about sex differences are of the form 'sex differences predict sex differences'. Such criticisms suggest that sexual selection theory does not properly engage with the definition of the sexes, and that additional, possibly biased sex-specific assumptions are made (Figure 1), thus precluding the inference that conventional sex differences arise from the definitional difference in gamete size. However, others argue that there are fundamental scientific reasons behind these classical views rather than gender biases [16–21].

The field of sexual selection therefore finds itself in an uncomfortable position, where some researchers are convinced that anisogamy underlies the evolution of typical sex differences, while

## Highlights

Sexual selection is both widely studied and widely debated.

We assess a central but criticised aspect of sexual selection theory: that is, the claim of a causal effect from gamete dimorphism to the evolution of sex differences.

Although a small number of recent models have explicitly analysed the causal link from gamete dimorphism to sexual selection, we find that the majority of models in sexual selection do not do so.

Critical questions and debates force researchers to look deeper into the foundations of theory, and to find ways to develop theory that bridges gaps in existing research.

Such research can be complementary to classical theory and stand alongside it, rather than replace it.

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**Box 1. Biological definition of the two sexes**

The majority of theoretical research in sexual selection does not present an explicit definition of the two sexes (see main text and Box 2). This can be problematic, because without a clear definition of the sexes it is difficult to pin down how sex-specific selection should operate, and what should be the fundamental underlying difference that drives it. If we are to make a first principles type of argument about the evolution of the sexes, in principle the only difference we should allow to be built into the model is the definitional one – otherwise we risk only showing that sex differences predict sex differences [9]. By specifying such sex differences without critically examining their link to anisogamy, we may also risk unconscious biases influencing the choice of such differences and assumptions.

Even if the aim is not to construct a theoretical argument connecting all the way to the definition, we argue that it is useful to include the definition in every paper on sexual selection. The definition is brief, and omitting it invites uncertainty regarding the logical consistency of the theory. Explicitly including the definition, however, serves as a reminder to carefully consider the assumptions the model might contain, beyond the definitional sex difference.

The biological definition of the two sexes is simple: biologically, the female sex is defined as the adult phenotype that produces the larger gametes in anisogamous systems, while the male sex is the adult phenotype that produces the smaller gametes [4,47].

A causal claim regarding the differential evolution of the sexes should therefore ideally either draw a causal argument from a difference in gamete size to the studied traits, or explicitly point out what are the additional assumptions being made, and provide a justification for them.

We emphasise that here we are specifically concerned with the biological definition of the sexes. The biological definition of sexes is intended to apply generally to sexually reproducing species, well beyond humans and helps us describe and categorise life on the broadest scale. As Griffiths [4] and Goymann et al. [3] note, the biological definition of the sexes is ill-suited for making decisions about the social or legal status of humans.

others are convinced of the opposite. At the same time, it is implied that most of the existing theory is ill-suited to even address these questions. It is therefore useful to assess the state of the field and consider potential ways forward. The goal of this paper is to quantify to what extent
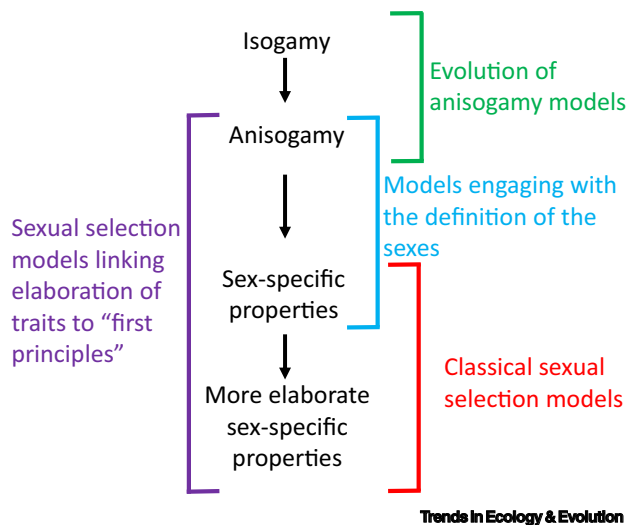


Figure 1. A heuristic scheme of models on sexual selection and evolution of the sexes. The majority of the models in our survey are closest to the red section, where assumed sex-specific traits or properties result in the further evolution or elaboration of sexually selected traits. The blue section illustrates how assumptions of sexual selection models (e.g., female demographic dominance) can be explicitly linked to anisogamy (the definition of the sexes). Note that although the red and blue models overlap in this diagram because they begin and end at sex-specific characteristics, respectively; this does not imply that those sex-specific characteristics are the same. That is, classical sexual selection models start from a set of sex-specific characteristics (e.g., choosy females and flashy males) that were chosen by researchers rather than causally derived from anisogamy, and it cannot be taken for granted whether models starting from anisogamy (blue area) causally connect to that same trait set. The purple section illustrates models which explicitly link anisogamy to the evolution of sexually selected traits. The evolution of anisogamy from isogamy (green) is typically modelled separately, but in principle there is no reason why the coevolution of anisogamy with sexually selected traits could not be modelled. This diagram is not intended to represent the entire sexual selection literature; for example, models that are symmetric with respect to the sexes but do not causally link to anisogamy do not straightforwardly fit into this diagram.

a representative sample of existing theory addresses the link between anisogamy and the evolution of sex differences. Is the logic of theory in sexual selection and the evolution of sex differences circular, in the sense of assumed sex differences predicting sex differences (as opposed to the definitional difference in gamete size predicting sex differences)? If so, to what extent is it a problem, and what can be done to meet these criticisms? We address these questions by surveying sex-specific assumptions and engagement with the definition of sexes in a broad sample of mathematical models in sexual selection theory, using two literature searches: one with no age limit, and another covering recent papers only. The aim is not to criticise any specific, existing study or its scientific value. Instead, the aim is to characterise the state of the field with a neutral sample. We discuss the special nature of sexual selection theory in terms of its assumptions and the expectations placed on them. We argue that the requirements on these assumptions depend on the nature of the question being addressed and discuss practices and ways forward which may alleviate disagreements and uncertainties regarding such models.

## Survey of sex-specific assumptions in sexual selection models

We analysed 400 papers in sexual selection following the protocol described in Box 2, with the aim of gaining a broad-scale quantitative understanding of the prevalence of sex-specific assumptions in sexual selection theory, and of the extent to which theory engages with the definition of the sexes. The overall results are presented in Box 2, and the selection of papers is given in the supplemental information online.

Unsurprisingly, some models are challenging to define completely unambiguously into categories, but the main outcome is clear: the majority of causal models in sexual selection theory do make sex-specific assumptions beyond the definition of the sexes, and do not clearly define the sexes. This applies to the all-time as well as the recent search.

Two specific types of sex-specific assumptions stood out as particularly common. The first is the preconception of choosy females and competing/displaying males, such that choosiness is allowed to evolve only in females, and correspondingly, a display trait is allowed to evolve only in males. The second common type of assumption is female demographic dominance, where female fecundity is independent of male abundance, while male reproduction is proportional to female abundance [22]. Although the question of conventional and unconventional assumptions is not the core topic of our study (see Box 3 for this distinction), in almost all cases the assumptions were conventional in this sense, as opposed to, for example, choosy males and displaying females. We discuss examples of models without sex-specific assumptions in Box 3, and methods for avoiding the assumption of female demographic dominance in Box S1 in the supplemental information online.

Given that most models started with sex-specific assumptions, and given that most do not present a definition of the sexes in the first place, they correspond most closely to the red section of Figure 1. Furthermore, although a few surveyed models did start from symmetrical initial conditions (i.e., without making sex-specific assumptions), most of these models nevertheless did not engage with the definition of the sexes.

## Assumptions in theoretical research and in sexual selection in particular

All models contain assumptions, or else they would not be helpful in providing a simplified and more digestible perspective on the world. George Box [23] wrote that all models are strictly speaking wrong due to their simplifying assumptions, but he also emphasised that the modeller should embrace this and seek an economical description of natural phenomena. Justification for an assumption might stem from it being a faithful representation of reality, or it may stem from

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**Box 2. Literature search protocol and results**

Our goal here is not to attempt to review the entirety of the vast literature on sexual selection but instead to seek a representative sample of theoretical papers, and to broadly characterise the nature of sex-specific assumptions and engagement with the definition of the sexes within those. To avoid a selection bias that is influenced by the authors' own knowledge of the field, we adapt the protocol of a recent article with a different, but conceptually analogous aim [52]. We searched for the top 200 Google Scholar results (in incognito mode) for all time, and for the past 10 years separately, using neutral and minimal search terms that preclude 'cherry-picking' the results. For the all-time search we used the search term 'sexual selection'. In the search covering the past 10 years only, theory papers tend to get swamped by the ever-growing diversity of sexual selection research, and for this more recent search we added the terms 'mathemat* OR model*'. The articles were further categorised into those that presented novel mathematical theory on sexual selection, and those that do not. The subset of mathematical papers (see Table S2 in the supplemental information online) was then categorised into theory on measurement of sexual selection, and theory presenting causal models that aim to illuminate the processes of sexual selection (i.e., models aiming to understand and explain sexual selection starting from some set of assumptions or premises). The specific theoretical method used in these papers was not in itself relevant in our survey, and could take many forms, such as population genetics, evolutionary game theory, simulations, and so on. To maintain a consistent, simple, and unbiased selection protocol, we excluded non-peer-reviewed sources, verbal models and reviews, because purely verbal descriptions may be ambiguous regarding assumptions, while reviews (if they contain mathematical models) may result in double-counting models.

Methods for measurement of sexual selection typically have no sex-specific assumptions and treat the sexes in identical ways. However, their nature is largely descriptive and they do not attempt to explain the evolution of sexually selected traits. The causal models are therefore the most informative for our survey. Of the causal models, regardless of the time-period, the majority do contain sex-specific assumptions of an asymmetrical nature, and a similar majority do not present a definition of the sexes.

Finally, the causal mathematical models were broadly classified into: (i) asymmetrical causal models with sex-specific structure in the equations; (ii) causal models with symmetrical equations for the two sexes but with asymmetric parameters with respect to the sexes reflecting sex-specific assumptions; and (iii) causal models where both equations and parameters are symmetrical but which can still predict differentiation of the sexes. We also checked if the articles containing mathematical models presented a definition of the sexes (Box 1).

The all-time search included 40 theory papers fulfilling our overall criteria (see Table S2 in the supplemental information online). Of these, ten papers were on methods for measuring sexual selection while 30 contained causal models of sexual selection. Further categorisations would of course be possible: for example, three of the causal models were models on speciation by sexual selection. The results for the past 10 years included 42 theory papers, one of which was categorised as measurement, and 41 as causal models.

Out of the 30 causal models in the all-time search, three define the sexes, 23 have asymmetric models, while seven contain either symmetric models or a mix of symmetric and asymmetric models. Out of the 41 causal models in the last 10 year search, four define the sexes, 38 have an asymmetric model, while three have a symmetric model or a mix of symmetric and asymmetric models. If we single out those published in the past 5 years, 21 of the 41 models remain, out of which one defines the sexes and three contain a symmetric model or a mix of symmetric or asymmetric models.

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purely practical considerations such as mathematical tractability. A good model should therefore contain simplifying assumptions, but they must be chosen with good judgement [24–26]. These general arguments apply to models of sexual selection as much as any other model, while sexual selection comes with some particular challenges.

## Assumptions versus sex-specific assumptions

If there is a consensus that all good models contain assumptions, why are models in sexual selection particularly controversial? One reason is that typically these models do not just contain assumptions, but additionally sex-specific assumptions [10]. That is, assumptions or simplifications that are not identical for females and males beyond the definitional difference between males and females (gamete size). For example, a model might assume from the outset that females have all their gametes fertilised while males compete to have their gametes fertilised; or that females have potential to evolve selectiveness over mates, while males tend to evolve elaborate displays to attract females. Such simplifications can significantly streamline the model and mathematical analysis, as opposed to deriving everything from more fundamental properties such as sex-specific

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**Box 3. Models without sex-specific assumptions**

The two most commonly repeated sex-specific assumptions in the models we analysed were choosy females–displaying males and female demographic dominance. While they are indeed common, both have been relaxed in previously published models. For example, [53,54] explicitly relax the assumption of female demographic dominance, while maintaining the choosy females–displaying males structure. The possibility of choosiness in both sexes has been explored [55–57]. While some of the aforementioned models treat the sexes symmetrically in that similar equations describe them, they do not explicitly link the causal chain of logic to gamete size and number (i.e., to the definition of the sexes: Box 1). For example, the symmetric model of [57] can answer questions like 'what are the consequences for the evolution of mate choice if offspring care is costly, or if one or the other sex varies more in quality?' but cannot link this answer directly to anisogamy. Some models have made explicit causal links to anisogamy, for example, by linking the evolution of sexually competitive traits explicitly to gamete size, with no other initial differences between the sexes [19]. The definition of the sexes is built into the model, showing how unequal gamete numbers due to anisogamy can result in unequal investment in sexually competitive traits with no other assumed sex differences. However, the model does not answer many other questions, such as that of mate choice: is there a causal connection from anisogamy to the evolution of choosy females?

Note that the two notions of (i) considering models with no sex-specific assumptions and (ii) considering models with unconventional or reversed assumptions are different. Although (ii) is valuable in itself and avoids stereotypical thinking, it nevertheless entails sex-specific assumptions. The majority of sex-specific assumptions made in sexual selection theory are undoubtedly conventional (e.g., choosy females and displaying males), but this is a different point than the one we focus on in this article. Even if the number of unconventional models was equal to the number of conventional models, both types of models would still be built around sex-specific assumptions and would not be able to address the link between the definition of the sexes and sex-specific evolution. Neither type of model would engage with the definition of the sexes (see Figure 1 in main text).

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gamete numbers, or as opposed to assuming both sexes have the potential to evolve selectiveness over mates as well as elaborate traits to attract mates. While simplifying assumptions are sometimes justified by observation and natural history, one can ask to what extent the assumptions in sexual selection theory can be based on observation of the current state of nature.

Taking the strictest view for the sake of argument, one could claim that the only acceptable sex-specific assumptions should be those that are in fact not assumptions at all, but definitional differences: a difference in gamete size and number (Box 1). Including other sex differences as assumptions in a model may leave gaps in logic [5]. Some researchers have voiced milder concerns, encouraging authors to reflect critically on assumptions of *a priori* sex differences and to avoid presenting them as facts [10].

## Models of sexual selection, but not of origins of sex differences

Given that most of the mathematical models in our survey do contain sex-specific assumptions, from a technical perspective one might indeed say that most models in sexual selection are of the type 'sex differences predict sex differences' [9] (models in the red section in Figure 1). Perhaps a more surprising finding is that in fact most models we surveyed do not explicitly define the sexes in the first place. It is then clearly true that such a model cannot, by itself, causally link evolved secondary sex differences to the definitional differences (i.e., to anisogamy; Box 1): from this strict perspective, the logic is indeed missing in much of the research in sexual selection as has been claimed [5].

However, it would be unwarranted to retrospectively apply such a strict criterion to the majority of models in sexual selection theory: most models do not aim to build a logical bridge all the way to the definitional sex difference (i.e., models in the purple section in Figure 1). It is a valid scientific question to consider, for example, how a genetic correlation between a male ornament and female preference for the ornament can lead to a runaway self-reinforcing process of ever-elaborating ornaments [27–29]. We might observe a peacock's exaggerated train and ask: can a runaway process cause the evolution of such exaggerated traits? Phrased in this way, the modelling question does not commit to circular logic. However, such a model alone would not tell us if and why and

how these evolving traits link to anisogamy, and if anisogamy provides the impetus for the evolution of stereotypical sex roles. Examining the logical foundations of the field and attempting to complement existing theory with work that explicitly does engage with anisogamy, challenging though it may be, can only be beneficial to sexual selection research.

Although we believe there is nothing wrong with individual studies modelling the evolution of elaboration of male traits through female preference, that does not imply that the field of sexual selection as a whole has not been affected by biases and conceptions of stereotypical sex roles. For example, the research questions selected for study as well as the interpretation of their results can, and undoubtedly have been, coloured by several factors: the most conspicuous phenomena and those most accessible to existing methods tend to be studied first, and in addition biases and conceptions of stereotypical sex roles can influence research and slow down discovery of new phenomena.

### Models of the origins of sex differences

Even if the majority of models in sexual selection cannot make a logical link to anisogamy, this does not mean that such a logical link does not exist. On the contrary, the fact that there tends to be a correlation between reproductive traits and the production of small or large gametes suggests there is a link and a pattern to be explained [16–18]. Similarly, one cannot rule out the existence of such a logical link by constructing models where other, externally imposed factors that are not linked to anisogamy drive sex-specific evolution ([30–32] – see also [5,16] for discussion). Attempts to link gamete size and anisogamy to sexual selection go back more than seven decades, when Bateman [33] made an early, explicit claim about the relationship between anisogamy and the strength of intrasexual selection: 'The primary cause of intra-masculine selection would thus seem to be that females produce much fewer gametes than males'. Bateman's experiments, however, could not provide evidence for this claim, and an explicit mathematical explanation for the link has been proposed only recently [34]. Trivers [35] proposed further early verbal links between anisogamy (phrased in terms of parental investment via gametes) and sex-specific evolution, but some of these were refuted on logical grounds [36]. Recently, there have been several attempts to make the connections between anisogamy and sex-specific evolution more explicit [19,34,37–39]. These models are represented by the purple section in Figure 1. For example, a model could include the influence of gamete size on gamete number, which influences fertilisation success (and demographic dominance), which in turn can influence selection on traits such as male–male competition [19].

### Theory under-represented in our survey

We carried out the survey using a protocol with generic search terms where we had minimal influence over the selected papers (Box 2). It is nevertheless interesting to consider the kinds of theory papers that were not extensively represented in this set. Perhaps the most striking aspect is that the selection of articles we found (particularly in the all-time search) is primarily concerned with precopulatory sexual selection, the form of sexual selection envisaged by Darwin [1]. However, overlooked by Darwin , postcopulatory (or postejaculatory) sexual selection has been called the sequel to Darwin's pre-ejaculatory sexual selection, with implications that rival those of precopulatory sexual selection [21]. Postcopulatory sexual selection as it has most commonly been studied comes in two forms: sperm competition [21] and cryptic female choice [40], which can be considered analogues of precopulatory male–male competition and female choice, respectively [21,41]. The less commonly studied egg competition [42,43] and cryptic male choice [44,45] are similarly absent in our sample of theoretical studies.

Another aspect of sexual selection research that is largely absent from the selection of articles is the evolution of anisogamy itself (green section in Figure 1); that is, the ancestral divergence from equally sized gametes (isogamy) to two different gamete sizes (anisogamy) [46–48].

Models of the evolution of anisogamy and of postcopulatory sexual selection would likely, and almost by definition, engage more directly with gamete-level properties and definitions. Similarly, a recent proposal to redefine sexual selection itself [49] engages directly with selection at the gamete level.

## Concluding remarks

Research in sexual selection has come a long way since the early work of Darwin [1], and the field is growing in terms of both empirical and theoretical research [2]. Critical views are common and maintain some uncertainty and debate in the field [5,7–10,12,50], while counterarguments are made in defence of sexual selection theory [16,17,20,51].

The conclusions of our survey are twofold. It is clear that the majority of theoretical sexual selection studies do make sex-specific assumptions that are not linked to anisogamy, and most do not present a definition of the sexes. However, while we agree that being clear and specific regarding sex-specific assumptions is important [10], we do not suggest that existing research is retrospectively invalidated for these sex-specific assumptions. There are many valid questions we can ask by starting from some set of sex-specific assumptions, such as the potential to evolve choosiness in females and a display trait in males. At the same time, it is important to be aware of the limitations of such models. The aforementioned setup may be able to demonstrate that male displays and female choice can become exaggerated in a runaway fashion. It cannot, however, by itself show that this runaway is ultimately causally linked to anisogamy – the sex-specific assumptions regarding display and choice evolution cut the causal tie to gamete size. To draw conclusions about the link (or lack of one) from anisogamy to runaway sexual selection, one would need to draw causal connections to anisogamy, ideally allowing both sexes to evolve exactly the same traits and allowing the model results to show if macrogamete producers evolve to be choosy and microgamete producers evolve displays (Box 3).

We are unaware of models that link the runaway mate choice question explicitly to anisogamy, but there have been several other recent attempts to be more explicit about the causal effect of anisogamy. For example, theory suggests that strictly male–male competitive traits evolve more readily in microgamete producers [19]. The link to anisogamy is less clear for parental care which seems to readily evolve in microgamete producers (males) according to one recent model [38], while another showed that female-biased parental care can evolve when coevolution with sexually selected traits is considered [37]. The asymmetry in Bateman gradients was recently shown to have a theoretical link to anisogamy [34], as hypothesised by Bateman [33]. However, much remains to be explored (see Outstanding questions), and these recent models only scratch the surface of the contested causal links from anisogamy to sex-specific selection.

From this perspective, the ongoing debates regarding sexual selection and its logical foundations are ultimately beneficial to the field. Regardless of whether one agrees that the field of sexual selection has serious problems and biases or not, pointing out weaknesses in the field can also point the way towards potentially overlooked aspects of the theory.

### Outstanding questions

To what extent are classical results in sexual selection explicitly derivable from anisogamy?

Is there a logical link between gamete size and selection for choosiness over mates (or gametes)? That is, if we model the evolution of mate choice from first principles (i.e., from anisogamy), do we find that anisogamy tends to consistently select one sex or the other to be choosier over mating partners or gametes? Under which conditions does the macrogametic sex become choosy, and under which conditions does the microgametic sex become choosy?

Is there a logical link between gamete size and selection for parental care? That is, are micro- or macrogamete producers more likely to evolve parental care, and how does this depend on internal versus external fertilization/fertilization probability/ecology (e.g., mortality rate during parental care)?

Are reversals of dominant patterns (e.g., male-biased parental care, female-biased mate competition, male choosiness, sex-role reversed sea horses, and other syngnathid fishes) consistent with the general theory of sexual selection from first principles? Why are they relatively rare, and how do they evolve?

## Declaration of interests

The authors have no interests to declare.

## Supplemental information

Supplemental information associated with this article can be found online https://doi.org/10.1016/j.tree.2023.04.013.

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