

SHORT COMMUNICATION

Mate-sampling costs and sexy sons

H. KOKKO*†‡, I. BOOKSMYTHE§ & M. D. JENNIONS*

*Centre of Excellence in Biological Interactions, Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Canberra, ACT, Australia

†Wissenschaftskolleg zu Berlin, Berlin, Germany

‡Institute of Evolutionary Biology and Environmental Sciences, University of Zurich, Zurich, Switzerland

§Animal Ecology, Department of Ecology & Genetics, Uppsala University, Uppsala, Sweden

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Abstract

Costly female mating preferences for purely Fisherian male traits (i.e. sexual ornaments that are genetically uncorrelated with inherent viability) are not expected to persist at equilibrium. The indirect benefit of producing 'sexy sons' (Fisher process) disappears: in some models, the male trait becomes fixed; in others, a range of male trait values persist, but a larger trait confers no net fitness advantage because it lowers survival. Insufficient indirect selection to counter the direct cost of producing fewer offspring means that preferences are lost. The only well-cited exception assumes biased mutation on male traits. The above findings generally assume constant direct selection against female preferences (i.e. fixed costs). We show that if mate-sampling costs are instead derived based on an explicit account of how females acquire mates, an initially costly mating preference can coevolve with a male trait so that both persist in the presence or absence of biased mutation. Our models predict that empirically detecting selection at equilibrium will be difficult, even if selection was responsible for the location of the current equilibrium. In general, it appears useful to integrate mate sampling theory with models of genetic consequences of mating preferences: being explicit about the process by which individuals select mates can alter equilibria.

Introduction

The occurrence of extravagant sexual traits, usually in males, is an obvious feature of the natural world. In some cases, these traits are functional weapons (e.g. horns and tusks). In other cases, they are, however, purely ornamental (e.g. elongated tails, elaborate song, bright plumage). It is widely accepted that ornaments have evolved under sexual selection driven by female mate choice. One problem with this explanation is that extravagant male traits seem to be most common in species where the rewards of choosiness for females appear to be smallest. Specifically, in nonterritorial species lacking male parental care, all that females appear to gain from males is sperm. The advantage of being

choosy therefore seems to be associated with genetic (indirect) benefits that elevate net offspring fitness. This has led to a theoretical challenge often referred to as the 'lek paradox' (Kirkpatrick & Ryan, 1991).

It is challenging to explain *costly* female mating preferences for ornamented males when females gain no direct benefits from choice. Fisher (1930) reasoned that choosy females indirectly benefit by producing 'sexy sons' (i.e. males with above-average mating success). Indirect selection on the preference is based on a genetic correlation that arises between the female preference and the preferred male trait: choosy females prefer ornamented males, and there is direct positive selection on the male trait when it confers a sufficiently strong mating advantage to outweigh reduced male survival. A breakthrough in sexual selection theory was the validation of Fisher's process using quantitative and population genetic models of preference–trait coevolution (Lande, 1981; Kirkpatrick, 1982).

Correspondence: Hanna Kokko, Research School of Biology, Australian National University, 116 Daley Road, Canberra, ACT 0200 Australia.
Tel.: +61 (2) 6125 6931; fax: +41 (0)44 635 57 11;
e-mail: hanna.kokko@ieu.uzh.ch

An assumption of these early models was that female choice is cost-free. This is an important assumption because once male trait expression reaches equilibrium, the indirect benefits of choosiness disappear. There is no longer additive genetic variation in fitness associated with the expression of the male trait. This occurs either because the trait goes to fixation, or, when variation in trait expression remains, there is a perfect trade-off between its beneficial effect on male mating success and its detrimental effect on male survival (Lande, 1981). The net result is that choosy females no longer produce fitter sons, which eliminates indirect selection for the mating preference. At this point, any costs of choosiness lead to direct selection against female mating preferences, which decline to their naturally selected optimum (usually assumed to be random mating). The male trait is consequently not maintained either.

The best-known solution allowing a costly mating preference to persist is to invoke biased mutation on preferred male traits, thereby maintaining indirect benefits of choice (Pomiankowski *et al.*, 1991). Biased mutation maintains additive genetic variation in fitness despite a directional mating preference. This demonstrates that Fisherian models *can* work when choosing is costly, but these costs have to be minute given realistic mutation rates. It seems that additional direct benefits and/or indirect viability benefits of choosiness are required (Maynard Smith, 1991; Kuijper *et al.*, 2012).

Frequency-dependent benefits are integral to female-choice models. Specifically, the magnitude of the mating advantage of ornamented males depends on the relative frequency of females with a mating preference that makes them more likely to mate with these males. Strangely, however, despite early theoretical discussion of how preference expression might depend on mate-sampling tactics (O'Donald, 1980; Seger, 1985), equivalent frequency-dependent costs of choosiness have attracted little attention. A notable exception is Pomiankowski (1988) who showed that frequency-dependent changes in the costs of mating preferences can alter equilibria. However, this early work made the verbal argument that because random mating with the first male encountered is the least costly option, it cannot be invaded by any other type of mate choice. Consequently, evolutionary competition between two types of *nonrandom* mating (preference for either ornamented or for nonornamented males) was modelled, such that preferences for the more common type of male were directly selected for. This study therefore deferred exploration of the crucial contrast between having a preference and mating randomly, which is at the heart of most mate choice evolution models (i.e. why preferences evolve when direct selection favours random mating).

We show here that frequency-dependent costs of choosiness merit reconsideration: even if direct selection

never favours preference alleles over random mating, the evolutionary dynamics do not always predict preference erosion. Costs can exist everywhere along the coevolutionary path towards the endpoint, which then, at equilibrium, features female choice that minimizes costs (as in Pomiankowski, 1988). Importantly, preferences can evolve upwards along this path despite there being (continually diminishing) costs, because benefits have not yet vanished either.

Empiricists emphasize that the costs of choosiness depend on the effort expended in mate searching and sampling: how long does it take, or how far must females travel, to find a suitable mate? Theoretical models, however, typically use fixed costs that depend only on whether a female carries a preference allele, or genes for greater expression of a preference (for an exception in a good genes context see Houle & Kondrashov (2002); in a speciation context see Gavrillets & Boake (1998) who include the cost of remaining unmated if the preferred male type is rare). We investigate a simple scenario where it proves important to take into account that the cost of a preference might change with the frequency of preferred males. This should affect how the net benefits of choosiness change during the coevolutionary process, with potential implications for evolutionary dynamics and for evolutionary stable outcomes.

The fact that theoreticians have tended to ignore how relative encounter rates with preferred and non-preferred males affect the costs of choosiness is a surprising omission, especially given the following statement by Andersson (1994, p. 43) in a book that almost every researcher working on sexual selection has read:

Preferences therefore may have a cost that is inversely related to the frequency of the preferred type of male. The dynamics and stability conditions of the system then change dramatically...

Despite this statement, the lack of research interest in this area is reflected in the fact that twelve of the thirteen well-known papers Andersson then cited (e.g. Lande, 1981; Kirkpatrick, 1982; Seger, 1985; Pomiankowski *et al.*, 1991) actually did not model frequency-dependent costs (the sole exception being Pomiankowski, 1988). This is intriguing because formal Fisherian models appeared simultaneously alongside a burst of research investigating how mate-sampling rules and preference functions affect mate quality (e.g. Janetos, 1980; Parker, 1983; Real, 1990). Subsequent work has not unified these subfields. Numerous theoretical studies have now considered the details of how mate sampling impacts the expected 'quality' (or trait value) of chosen males (Sullivan, 1994; Luttbeg, 1996; Mazalov *et al.*, 1996; Wiegmann *et al.*, 1996, 2010a,b, 2013; Johnstone, 1997; Hutchinson & Halupka, 2004; Wiegmann & Angeloni, 2007), but these appear not to

have influenced theoretical work on the coevolution of preferences and traits. Even papers that involve mate-sampling costs (e.g. Houle & Kondrashov, 2002) rarely cite this parallel literature as a source of inspiration.

What would have happened if mate sampling theory had been formally incorporated into early Fisherian mate choice models? Here, we show that it might have discouraged the textbook dogma that Fisherian benefits cannot, even in principle, sustain mating preferences if they impose costs (e.g. Cameron *et al.*, 2003). In the context of female choice for 'good genes' (i.e. male viability indicator traits), a model that explicitly considered changes in mate-sampling costs (Houle & Kondrashov, 2002) yielded different conclusions to those reached with a model invoking fixed costs of mating preferences (Kirkpatrick, 1996) (although note that there are additional differences between these models).

Our aim here is to construct a parallel comparison between an early model of Fisherian evolution (Kirkpatrick, 1982) and an approach that derives costs through explicitly modelled mate sampling. We do this in two ways: (i) by a two-locus model with all assumptions identical to early work, apart from introducing costs of choice that are based on explicit mate sampling, and (ii) by building an individual-based model that relaxes many potentially restrictive assumptions at once. We show that when choosy females pay smaller search costs as preferred males become more common, the outcome of preference–trait coevolution models changes dramatically. Contrary to early suggestions (Pomiankowski, 1988), this can happen even if choice is never cheaper than random mating.

Materials and methods

Model 1: a two-locus model

Kirkpatrick (1982) provided a simple way to model indirect benefits given a female preference (P) for a male display trait (T) that reduces male viability. We follow this general approach. We assume a haploid population with discrete generations. Individuals of both sexes have two loci; one determines the presence (T_1) or absence (T_0) of a male-only display trait, the other determines whether a female preference for T_1 males is present (P_1) or absent (P_0). Females mate once. The display trait is costly: the viability of T_0 males is 1 and that of T_1 males is $1 - s$ ($s > 0$). Both indirect and direct selection act on female preferences. We consider three versions:

(a) *Full model*: Following suggestions that realistic mate choice might only involve sampling a few males (Roff & Fairbairn, 2014), we assume P_1 females sequentially sample up to five males, whereas P_0 females mate with the first male encountered. If q is the frequency of

T_1 males after viability selection, the probability that a P_0 female mates with a T_1 male is q . For a P_1 female, we assume that she mates as soon as she encounters a T_1 male, but if this has not happened by her fifth mating encounter, she accepts the current (T_0) male. Hence:

$$\text{Prob}\{\text{sire is } T_1 | \text{female is } P_1\} = q + (1 - q)q + (1 - q)^2 q + (1 - q)^3 q + (1 - q)^4 q. \quad (1)$$

A P_0 female pays no cost of choosing as she always mates with the first male encountered. For a P_1 female, the cost of choosing depends on how many males she samples before mating. The full cost (denoted c) is paid only if she mates with the fifth male encountered, whereas there is no cost if she mates at her first encounter (i.e. the same as for a P_0 female). Assuming additively accumulating costs per sampling event, the expected cost for a P_1 female mating with a T_1 male is

$$C = \frac{\frac{c}{4}(1 - q)q + \frac{2c}{4}(1 - q)^2 q + \frac{3c}{4}(1 - q)^3 q + c(1 - q)^4 q}{\text{Prob}\{\text{sire is } T_1 | \text{female is } P_1\}}. \quad (2)$$

A P_1 female mating a T_0 male must have sampled five males, so her cost is always c .

(b) *Hybrid model*: sire identity is determined following the full model. P_0 females again pay no sampling cost, but P_1 females always pay the full cost c . Because the hybrid model combines an explicit sampling process with the assumption of classic models of female choice that costs of choosiness are unavoidable, comparing the outcomes of the hybrid model with the full model and the classic model helps to disentangle the independent roles of cost frequency-dependence and the effects of sampling on mate choice evolution.

(c) *Classic model*: a P_1 female mates with a T_1 male with probability

$$\text{Prob}\{\text{sire is } T_1 | \text{female is } P_1\} = \frac{aq}{aq + (1 - a)}, \quad (3)$$

where a is equivalent to a_2 in Kirkpatrick (1982) (one interpretation is that a P_1 female is a times more likely to mate a T_1 than T_0 male in a two-choice test). The probability that a P_0 female mates with a T_1 male is q . All P_1 females pay the full cost c .

The models track genotype frequencies in each generation (see Appendix), assuming the order: (1) viability selection on T_1 males; (2) females choose mates; (3) females breed (given a cost C or c , female fecundity is multiplied by $(1 - C)$ or $(1 - c)$); (4) parents die. We also included an option at step (4) for biased mutation converting T_1 to T_0 (i.e. trait loss) at the rate μ . This allows us to contrast our results with models where biased mutation maintains female preferences (Pomiankowski *et al.*, 1991).

Model 2: an individual-based simulation

Kuijper *et al.* (2012) review four different approaches to implementing the Fisher process. To check whether the gist of our argument based on the simplest approach holds, we use the last, and most complex, approach: an individual-based simulation (see also Roff & Fairbairn, 2014). The most important assumption to relax is the dichotomous nature of ornaments and preferences. In the individual-based simulation, each individual is characterized by its sex, by 100 haploid loci with alleles 0 or 1 for an additive male trait T (expressed only in males), and one haploid allele that takes positive integer values and specifies the female preference threshold P (expressed only in females). We assume a mutation rate μ for the female preference and $\mu/100$ for each locus of the male trait (thus leading to the same overall mutation pressure for preferences and traits alike). Female choice requires that males exceed a threshold trait value: a female with preference P will mate with males whose sum of allelic values is at least P . Mate sampling occurs as in the full and hybrid two-locus models, with costs accumulating in the same way such that females who reach the maximum number of mates sampled (N) pay the highest cost. As a further check of robustness, we combine results derived with $N = 5$ (as

in the two-locus models) with others that use $N = 10$. Details of the model are given in the Appendix S1.

Results and discussion

As in all Fisherian models, the mating preference must initially exceed a threshold frequency (invasion barrier) to increase and be maintained by indirect selection (Fig. 1: green area). We considered six scenarios in the two-locus model (the full, hybrid and classic model variants, either with or without biased mutation on the male trait). For easier visualization in Fig. 1, we use relatively large values for both the maximum cost of the female preference ($c = 0.01$: sampling five males reduces female fecundity by 1%) and the cost of the male trait ($s = 0.4$: T_1 males have 40% lower survival). Smaller costs lower the invasion barrier to preference (and trait) increase and maintenance. For example, if $c = 0.001$ and $s = 0.1$, an initial preference prevalence of 4% is sufficient to lead to trait maintenance (if the male trait has $\geq 2\%$ prevalence initially).

We first consider what happens without biased mutation on the male trait. When sampling costs decline as the frequency of preferred T_1 males increases, the male trait goes to fixation if the initial frequency of the preference exceeds the invasion barrier (the full model,

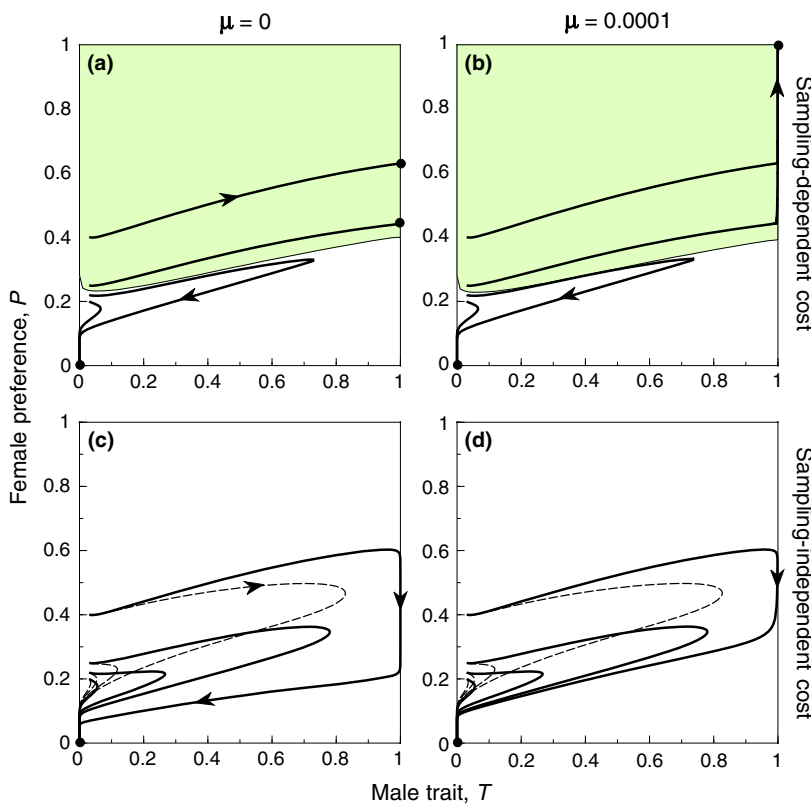


Fig. 1 Frequencies of preference allele (P_1) and T_1 males after viability selection in the two-locus models. Evolutionary trajectories (arrowed lines) always start from the same four representative points. Solid circles indicate evolutionary endpoints (equilibria). The full model output is in (a) and (b), showing that the system can equilibrate with positive traits and preferences. The green area indicates initial combinations that generate a coevolutionary increase in P_1 and T_1 towards such equilibria. Such combinations are completely absent in the hybrid model (solid lines) and classic model (dotted line), depicted in (c) and (d): thus, constant costs rather than the effect of sampling on mate identity is responsible for the difference in outcome. Biased mutation on male traits is either absent (a, c) or present at $\mu = 0.0001$ (b, d).

Fig. 1a). At equilibrium, there is no direct selection on the mating preference: *all* males are of the preferred type, so both P_0 and P_1 females mate with the first male they encounter. As T_1 is fixed, there is also no longer indirect selection on the preference allele. This results in a neutral line of equilibria (see Appendix). In contrast, when sampling costs are independent of the frequency of T_1 males, a costly preference, and hence costly male display, cannot persist at equilibrium (both the classic and hybrid models, Fig. 1c). The crucial difference is therefore due to the frequency-dependence of the costs of choice and not to how the mate-sampling tactic determines mate identity: although the hybrid model uses an explicit sampling process, the fixed cost of choosiness ensures neither the preference nor trait persist.

A purely Fisherian process (indirect selection on a mating preference arising solely from linkage disequilibrium with a preferred male trait under direct selection) can thus maintain a costly male sexual display even when the preference carries costs due to active mate sampling and when random mating is included as a 'cheap' alternative. Previously, the evolutionary stability of a preference for such Fisherian traits has only been demonstrated when there is biased mutation on the male trait (e.g. Pomiankowski *et al.*, 1991).

In the individual-based model, where we relax the assumption that male traits and female preferences are dichotomous variables, the preference thresholds used by females evolve to be consistently below the mean of the male trait distribution (see the Appendix S1). Preferences and traits coevolve until they drift along a line that appears – to the extent that it is possible to deduce this from an individual-based simulation – neutral. In the depicted trajectories of Fig. 2, we found no evidence of preference decay, and neither were collapsing cases found when we tried starting simulations from 50 randomly chosen parameter settings (Fig. 2, shaded area gives evolutionary endpoints). Although the dynamic consequences of a preference threshold clearly differ from those arising from the simpler preferences implemented in the full two-locus model, the findings of both models are consistent with our general interpretation: preferences can evolve upwards when both benefits and costs are significant, and this directional evolution stops once males have evolved to 'satisfy' female preferences and costs have become irrelevant.

We are aware that it is tempting to dismiss our findings as somehow trivial because the mating preference becomes cost-free at equilibrium. We argue that this would be uncharitable as: (i) the preference imposes costs at *every* point on the evolutionary trajectory towards equilibrium, so the situation modelled is not analogous to that of classic cost-free models (e.g. Kirkpatrick, 1982); (ii) the biological reality is that preference costs are rarely independent of the frequency of preferred males, so it is an artificial con-

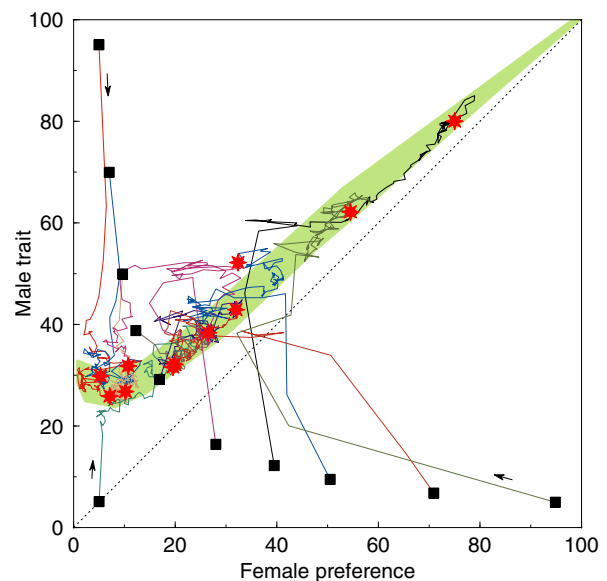


Fig. 2 Coevolution of female preference thresholds and male traits in the individual-based simulation, with $c = 0.01$, $\mu = 0.01$ and either a maximum of $N = 5$ sampled males (11 depicted trajectories) or $N = 10$ (the 50 trajectories are not depicted, instead the green-shaded area covers all evolutionary endpoints). We depict 11 trajectories that start at the black squares as indicated (to cover a range of values where either the preference or the trait is not yet strong) and end at the red stars at generation 10 000. For clarity in a simulation that was run for 10 000 generations per trajectory, the lines track the mean allelic values of each population only every 100 generations. To increase the robustness of the conclusion that simulations do not collapse, and that preferences and traits can coevolve to higher values their initial starting values, we ran our $N = 10$ (maximum number of males sampled) examples from random starting points: each case was started such that mean female preference threshold was randomized to be between 0 and 50, and mean male traits were between 0 and 90. None of the outcomes at generation 10 000 were found outside the green-shaded area. The overall conclusion is that all populations evolve to spend much of the evolutionary time near a line where the mean male trait values somewhat exceed the mean threshold mating preference values; some populations evolve males with strongly compromised survival (male traits higher than 75 lead to more than 50% male viability reduction, and 8 of 50 random runs exhibited such values at generation 10 000; 2 of these had the trait persist at its maximum where all 100 male trait alleles had the value 1).

struct to maintain a cost where none would exist; (iii) it is not obvious *a priori* that the rate at which direct selection against a preference declines can be *greater* than the rate at which indirect benefits decline (due to less variation in attractiveness as T_1 approaches fixation); (iv) intriguingly, the model accounts for male traits persisting despite no current advantage to choosiness.

We next consider what happens given biased mutation on the male trait. In the examples presented

(Fig. 1b,d), the mutation rate is low ($\mu = 0.0001$). When sampling costs decline as preferred T_1 males increase in frequency, becoming easier to find, there are only two equilibrium points (the full model, Fig. 1b). Again, if the initial preference frequency lies below the invasion barrier, the preference and trait are eliminated. If above the invasion barrier, however, the preference becomes fixed and the male trait almost reaches fixation (the proximity depends on μ : the lower it is, the closer the trait is to fixation). The indirect benefit of choosiness (due to variation in male genotypes, $q < 1$) exceeds, in this example, the strength of direct selection, so the preference increases in frequency until it reaches fixation. Again, it was unclear *a priori* that the relative rate of decline in direct selection could exceed that of indirect selection.

It is well established theoretically that biased mutation can sustain a costly preference (Pomiankowski *et al.*, 1991). In our example, a frequency-independent cost of choice eliminates both the preference and male trait (the hybrid and classic models, Fig. 1d). Of course, we emphasize that this would not have occurred had we used a sufficiently high mutation rate. The point we wish to make, however, is that a mutation rate too low to maintain a preference with a fixed cost (Fig. 1d) can maintain it when costs are explicitly derived from mate sampling theory (Fig. 1b).

Our model does not explain how a mating preference initially increases in frequency to exceed an invasion barrier. Nor does it fully resolve the lek paradox (why females are choosy if choice depletes variation), as it ignores nonadditive and environmental factors that affect male trait expression. This is a potential limitation of the model because such factors reduce indirect selection on the mating preference (i.e. choosy females less often acquire fitter sons), but it should be noted that most models of preference–trait coevolution similarly avoid this complication.

For empiricists, it is worth reflecting on the difference in observations when viewing a population moving towards equilibrium (A) and another already at equilibrium (B). In A, it is possible to detect costs of choosiness that are up to 1% of a female's fecundity and observe that the mating success of sons depends on their father's genotype (T_0 or T_1). In contrast, in B, all males have a costly trait, and most (Fig. 1a) or all (Fig. 1b) females have a cost-free mating preference for this trait (demonstrable by experimental manipulation of trait expression to induce the requisite variation). Despite this, there is no measurable advantage for the sons of females that mated with preferred males. It would obviously be puzzling to field researchers as to why females have evolved to prefer ornamented males in population B.

Our model is a reminder that variation among males in the evolutionary past could have created coevolutionary forces that drove female preferences to their

current levels, where they are now hard to explain. Preferences become non-neutral again, re-establishing indirect selection and observable trait–preference coevolution, as soon as populations are pushed to the interior of Fig. 1. This would occur, for example, if increased mutation rates reduce the male trait. It is possible that empirical observations of female choice for currently non-beneficial male traits partially reflect 'the ghost of selection past'.

In sum, much of the frustration in testing sexual selection theory hinges on the prediction that direct selection against mating preferences easily outweighs indirect selection to mate nonrandomly. Our results reinforce this message: minute differences in direct costs affect our ability to explain male traits (e.g. the classic two-locus model; Fig. 1), but our models also include cases where predictable variation in costs becomes essential for the maintenance of a preference.

The as such correct statement, that it is difficult to explain costly female choice for indirect benefits, should therefore be accompanied by reminders that the magnitude of benefits *and* costs can change dynamically during preference–trait coevolution and that these changes do not necessarily occur at the same rate. If costs diminish faster than benefits, the evolutionary outcome can be far more choosiness than if the opposite is true. For empiricists, there is obvious potential to quantify the magnitude of frequency-dependent changes in the costs of choosiness by experimental manipulation of the frequency of different male types. One of the key messages, however, is that this might be a difficult task: we predict preferences will persist precisely where evolution has led the currently expressed costs to be minimal.

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Appendix

Our two-locus model largely follows the derivation of Kirkpatrick (1982), which is beautifully explained in expanded form (including mutations) in Chapter 2 of Rice (2004).

Populations in Fig. 1 are initialized assuming no linkage disequilibrium. Thus, if the initial frequency of the preference is assumed to be x and that of the male trait to be y , genotype frequencies in the initial generation are as follows:

$$P_{00} = (1-x)(1-y), p_{01} = (1-x)y, p_{10} = x(1-y), \\ p_{11} = xy,$$

where the first subscript denotes the value of the P allele, and the second refers to the T allele. Each generation then first applies viability selection, which modifies the frequency of T_1 males in the current generation to

$$q = \frac{(1-s)(p_{11} + p_{01})}{(1-s)(p_{11} + p_{01}) + (p_{00} + p_{10})}.$$

This value of q is then used to calculate mate identities and costs paid by females (equations 1–3 in main text).

Thereafter, offspring production follows the probabilities of each female finding a sire of each genotype and Mendelian laws of genetics. Consider, for example, the production of P_1T_1 offspring (the bookkeeping for the three other offspring types proceeds similarly). All matings between P_1T_1 females and P_1T_1 males lead to P_1T_1 offspring (before mutation). But so do half of the offspring produced in matings between P_1T_1 females and P_1T_0 males, between P_1T_0 females and P_1T_1 males, between P_0T_1 females and P_1T_1 males or between P_1T_1 females and P_0T_1 males. Finally, one quarter of the offspring produced by P_1T_0 females mating with P_0T_1 males and of matings between P_0T_1 females mating with P_1T_0 males, also become P_1T_1 . The proportions are multiplied by $1-c$ or $1-C$ where relevant: for example, neither cost applies to P_0T_1 females mating with any kind of male.

Thereafter, mutations occur: a proportion μ of P_1T_1 (P_0T_1) offspring become P_1T_1 (P_0T_0). After normalizing, the new generation is ready.

The model yields, in principle, an analytic expression for the change of allele frequencies, but in the interior of Fig. 1, the expressions are too unwieldy to yield much insight and are not reproduced here (the Mathematica file is available upon request). However, they simplify to zero when assumption set (a) is combined with $p_{01} = p_{11} = 0$, which indicates that the female preference becomes neutral when the male trait is fixed. This makes intuitive sense, as in that case, the realized mating behaviour does not differ between choosy and randomly mating females (neither in terms of mate identity nor the sampling effort taken).

Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Details of the individual-based simulation.

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