Fixed and dilutable benefits: female choice for good genes or fertility

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Benefits accruing to females who exercise mate choice have been defined to be either ‘direct’ or ‘indirect’. We suggest an alternative distinction: benefits can be considered ‘fixed’, meaning they are on average equal to all females mating with the same male (e.g. good genes’ benefits) or ‘dilutable’, meaning they are shared between females mating with the same male, so that the more mates a male has, the lower the average benefit to each (e.g. fertility benefits or many forms of direct benefit). Using a simple model, we show that this distinction has a major effect on the form of female preference. We predict that mating skew will be far greater in species where the benefits are fixed when compared with those where the benefits are dilutable.

**Keywords:** sexual selection; mate choice; good genes; phenotype-linked fertility; sperm; female preference

1. INTRODUCTION

The purpose of female mating preferences for male ornaments has been a subject of debate since Darwin’s time \cite{1,2}. Many hypotheses have been put forward which suggest the types of benefit accruing to a female from carefully selecting her mate. These benefits are generally categorized as being either ‘direct’ or ‘indirect’ in nature \cite{3,4}. Examples of direct benefits include getting more or high-quality food or territory from the male, a larger nuptial gift when mating, good parenting skills (for review of these, see \cite{2}) and high fertilizing efficiency \cite{5,6}. Alternatively, female mating preferences could have direct benefits owing to genes underlying them having beneficial pleiotropic effects elsewhere in the phenotype \cite{4}. Indirect benefits, on the other hand, are those that give an advantage to the female’s offspring rather than directly to her. Examples are having offspring with high genetic viability owing to ‘good genes’ \cite{7} or ‘compatible genes’ \cite{8}, avoiding the cost of inbreeding \cite{9,10}, or having attractive offspring (sometimes called the ‘sexy son’ hypothesis, originally proposed by Fisher \cite{11}). As the different benefits to females are not mutually exclusive, neither are the hypotheses. After much empirical and theoretical work \cite{3,12–16}, there is still debate as to the strength of evolutionary force generated by each type of benefit \cite{3,13,17,18}, and difficulty in empirically measuring the strengths of each force \cite{19–21}.

Another way in which potential benefits differ that has been overlooked in previous discussions is whether or not benefits can be shared. Consider the difference in this regard between the ‘good genes’ hypothesis \cite{22,23}, and the ‘phenotype-linked fertility’ hypothesis \cite{5}. The ‘good genes’ hypothesis postulates that females select their mates based on genetic quality, so as to have high-viability offspring. A male passes on an equal number of high-viability genes (on average) every time he mates, and so the expected benefit a female gets from mating with a given male is not dependent on the number of copulations he has with other females. A high genetic quality male will pass on high-quality genes in every mating (to first approximation, at least). We call this type of benefit ‘fixed’.

Now consider the ‘phenotype-linked fertility’ hypothesis. This postulates that females select males who have a higher fertilizing ability \cite{5}, to minimize the probability of unfertilized eggs. Fertilizing ability may depend on the number of mates a male has obtained: if males are sperm-limited, those that are preferred and thus mate many times will have a decreased expected ejaculate investment per mating, owing to depletion \cite{24,25}. A highly fertile male may ejaculate a large number of sperm the first time he mates, but this number will decrease as he has more matings \cite{6}. Thus, the expected fertility benefit a female gets from a given mate depends on the number of previous copulations he has had with other females. As the number of other females he mates with increases, the expected benefit to the focal female decreases. This effect will be exacerbated on an evolutionary timescale because there will also be selection for more attractive males to invest fewer sperm per mating \cite{26}. In this case, the benefits a male confers are ‘dilutable’.

This new distinction is not suggested as a replacement for the old direct/indirect categorization, but rather as an additional factor to consider in the field of mate choice evolution. The fixed/dilutable dichotomy has a bearing upon female behaviour, as we show using a simple model. In turn, this can affect mating skew, affecting...
the strength of sexual selection. A fresh look at categorizing female preferences may thus provide impetus for new empirical and theoretical investigations, and potentially shed further light on the evolution of mate choice.

To show that this new categorization of female benefits will affect mate choice behaviour, we consider optimal female preference in two idealized circumstances. In the first, females are selecting for good genes, and thus the benefits to be gained from higher quality males are fixed. In the second, females are selecting for high sperm count in ejaculates. Males are assumed to be sperm-limited, and so the benefits to be gained from higher quality males are dilutable. By contrasting these two cases, we show that there is potential for female behaviour to provide evidence of what benefits inform female preferences.

2. THE MODEL

We model an idealized species. All females are identical in terms of expected number of matings. The differences in fitness come from the female’s preference function, as this leads to differences in realized mating outcomes. By selecting a mate appropriately, a female can acquire benefits, either having more offspring (perhaps because her mate provides fertility benefits), or having more offspring survive to breeding age (perhaps because her mate provides more resources for the offspring, or has good or compatible genes). We assume that females cannot directly assess the benefits they wish to maximize when selecting a mate, but rather make decisions based on some male trait, characterized by a single real variable \( z \). This may be a single male trait, such as tail length, or it may be a combination of several traits, in which case \( z \) can be taken to be some suitable weighted average. We assume that there are lower and upper bounds on \( z \), which we denote as \( a \) and \( b \), respectively, so that for every male, \( a \leq z \leq b \).

For simplicity, we assume that choice is cost-free, so females can examine all possible males before making their decision. We also assume that there is a large density of available males of every trait value, and the duration of copulation is short relative to its frequency, so that copulation with a single male of trait value \( z \) does not significantly decrease the number of \( z \)-males in the mating pool. Females exhibit preferences based on \( z \). We model female preference as a function \( p(z) \), defined for \( a \leq z \leq b \), and satisfying \( p(z) \geq 0 \). Because we are interested in female preference as a relative measure (i.e. the attractiveness of trait value \( z_1 \) compared with that of trait value \( z_2 \)), we scale the preference function such that

\[
\int_a^b p(z) \, dz = 1. \tag{2.1}
\]

Thus, the preference function can be regarded as a probability density function describing the probability that a female will mate with a male whose trait value is within a given interval. We now define the expected benefit that accrues to a female depending on her preference function. The form this takes will differ depending upon the nature of the benefit at stake.

(a) Good genes (fixed benefits)

In the first case, females select a mate so as to maximize the genetic quality of their offspring. In this way, they improve the chances of their offspring surviving to breeding age. This is assumed to be dependent on the genetic quality of the male. We define the continuous benefit function, \( s(z) \). This is the expected benefit accruing to a female should she mate with a male of trait value \( z \). Of course, a male’s trait value is a noisy indicator of his actual quality, as trait values are affected by both genetics and environment; in particular, not all males of trait value \( z \) will have the same ‘good genes’. However, the female’s expected benefit \( s(z) \) is taken as an average across all \( z \)-males.

A female with preference function \( p(z) \) will then obtain expected benefit

\[
W[p] = \int_a^b p(z)s(z)\,dz. \tag{2.2}
\]

The preference function \( p \) that maximizes [2] will therefore be the function that maximizes female fitness \( W[p] \) in the ‘good genes’ case.

(b) Fertility (dilutable benefits)

In this case, females attempt to maximize fertilization of their eggs when they select a mate. This is assumed to depend on the number of sperm that the male transfers during mating. We assume that males suffer sperm depletion, so that the mean number of sperm transferred per mating decreases as the number of matings obtained by a given male increases (one way in which this assumption would be justified would be if the breeding season was short and intense, so that females who mated later with a given male never received more sperm than those who mated earlier, and sometimes received fewer sperm owing to short-term depletion). Thus, the expected benefit a female will obtain from mating with a male will depend on how attractive that male is considered to be by other females in the population, as well as on his trait value \( z \). Denote the average female preference function by \( p \), so that the average preference for a trait value \( z \) is \( p(z) \). We will call this the ‘popularity’ of trait value \( z \), and refer to \( p \) as the popularity function. We assume that the higher the popularity of a trait value, the more matings males bearing that trait value are likely to get, and thus the fewer sperm they will transfer per mating on average (for a fuller justification, see electronic supplementary material, appendix 1). Therefore, the expected benefit conferred on a female by a given male is a function of both his trait value \( z \) and his popularity \( q = p(z) \). We denote this trait-specific expected benefit by \( s(z,q) \), and assume that this function is continuous in both \( z \) and \( q \), and is positive for all pairs \( (z,q) \). Then a focal female with preference function \( p \) in a population with popularity function \( p \) will obtain the expected benefit

\[
W[p,p] = \int_a^b p(z)s(z,p(z))\,dz. \tag{2.3}
\]

This benefit function is linear in \( p \) but not (in general) linear in \( p \).

We want the benefit function \( s(z,q) \) to obey two conditions. First, we assume that the more matings a male gets, the fewer sperm on average he ejaculates per mating:
(i) Condition (i)
For each trait value \( z \), \( s(z, q) \) is differentiable in the popularity variable \( q \), and
\[
\frac{\partial s}{\partial q}(z, q) < 0,
\]
for all \( q > 0 \). That is, the benefit function is monotonically decreasing in \( q \), so that for fixed \( z \), the benefit function \( s(z, q) \) declines as the popularity \( q \) of \( z \)-males increases. This is because as a male’s popularity increases, he will mate more often, and thus the benefits that he confers will be shared between more females, meaning a lower expected share to each female. We also require that \( s(z, q) \rightarrow 0 \) as \( q \rightarrow \infty \), so that, if female preference for a male of trait value \( z \) increases indefinitely, then the reward to any particular female from mating with such a male diminishes to insignificance (the male has only a finite sperm reservoir to share among all his female mates).

Second, we also want to assume that males with larger trait values give larger benefits (i.e. more sperm) all else being equal (the phenotype-linked fertility hypothesis [5]). So the benefit function must also satisfy:

(ii) Condition (ii)
\[
\frac{\partial s}{\partial z}(z, q) > 0,
\]
for all \( q \geq 0 \). That is, the benefit function is monotonically increasing in \( z \) for fixed \( q \), so that if there are two males of equal popularity, the male with the larger trait value will confer higher benefits.

(c) Difference between the two models
The key difference between the two models is that for fixed benefits, the benefit function is dependent only on a male’s ornament. For dilutable benefits, however, the benefit function is dependent both on a male’s ornament and also on the mean preference function of the female population. This means different approaches must be used in the analysis of these two models: in the fixed case, we simply use an optimization approach, while in the dilutable case, we require an evolutionarily stable strategy (ESS) approach [27].

3. RESULTS
(a) Good genes (fixed benefits)
We look for benefit functions \( p(z) \) that maximize the expected payoff function \( W[p] \) given by equation (2.2).

Any preference function \( s(z) \) must attain a maximum value \( \tilde{s} \) at least at one point which we denote \( \tilde{z} \), so that \( \tilde{s} = s(\tilde{z}) \). Then we can define \( q_\tilde{s} \), a preference function that is a delta function \( q_\tilde{s}(z) = \delta(z - \tilde{z}) \), so that \( q_\tilde{s}(z) = 0 \) for all \( z \neq \tilde{z} \), and equation (2.1) holds for \( p(z) = q_\tilde{s}(z) \).

In other words, females with preference function \( q_\tilde{s} \) will only mate with males of trait value \( \tilde{z} \). The fitness of this preference function is:
\[
W[q_\tilde{s}] = \int_{a}^{b} q_\tilde{s}(z)s(z)dz = s(\tilde{z}) = \tilde{s}.
\]

Since \( \tilde{s} \) is the maximum value attained by \( s(z) \) on \([a, b] \), \( q_\tilde{s} \) is at least jointly optimal, since for any preference

function \( p \),
\[
\int_{a}^{b} p(z)s(z)dz \leq \int_{a}^{b} p(z)dz = \tilde{s},
\] (3.1)

using equation (2.1). The two sides of equation (3.1) will be equal (and thus \( p \) optimal) if and only if \( p(z) = 0 \) almost everywhere on the (open) set of points \( z \) for which \( s(z) \neq \tilde{s} \).

The optimal preference functions for females will therefore split males into two groups: the best, and the rest. Only males with the best genes will gain (consensual) matings; all others will be rejected by females. Any preference function that rejects all males who give less than the maximum benefit will be optimal. Mathematically, this means any preference function with \( p(z) = 0 \) for all \( z \) with \( s(z) < \tilde{s} \). If there is only a unique, optimal male trait value \( z^* \) that maximizes \( s \), there will be a unique optimum preference function, which will be a delta function \( q_{z^*} = \delta(z - x) \) (figure 1). More generally, the optimal female preference function will be indifferent between all those male trait values \( z \) for which \( s(z) = \tilde{s} \) (figure 2).

In the natural world, then, if preference is for good genes, all females should choose to mate with the same optimal male type (or possibly with males from a set of types conferring approximately equal benefits), who will therefore monopolize all (consensual) matings. Males with genes worse than the optimum (as signalled by their trait values) will be rejected. Given a choice between two males, females should always choose the male with the better genes.

(b) Fertility (dilutable benefits)
Here we consider a popularity function \( \hat{p}(z) \) which defines an ESS with respect to the benefit function \( W[p, \hat{p}] \) defined in equation (2.3).

We apply the well-established concept of an ESS; that a population, all of whose members use the same ‘equilibrium strategy’, denoted \( p^* \), should be resistant to invasion by a sufficiently small influx of mutants using a different strategy, denoted \( p \). This notion has been extensively developed in the context of finite strategy games [27]. The situation for games with infinite strategy spaces, such as in the dilutable
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4. DISCUSSION

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Figure 2. Another example of female preference for fixed benefits. A fixed benefit function \( s(z) \) is shown plotted against trait value \( z \). It attains its maximum for trait values \( a \leq z \leq b \). The optimal female preference function \( p(z) \) is zero for all \( z < c \), and thus females should reject any male with a trait value in this range. The preference function is constant and non-zero for trait values \( z \geq c \), and hence the expected payoff to each female will be zero in this range. Females are indifferent if given a choice between males with trait sizes larger than \( c \).

benefits case considered here, is somewhat more problematic, and more so when payoff functions are nonlinear. Here, we shall require that an ESS be a totally uninvadable strategy \([28,29]\) in the following sense:

\[
W[p'|(1 - e)p^r + ep] > W[p|(1 - e)p^r + ep]
\]

for all \( 0 < e \leq 1 \), and all alternative strategies \( p \neq p^r \). This means that, if we begin with an initial population of females who all use the strategy \( p^r \), and replace a non-zero fraction of the population with a subpopulation of females who all use an alternative strategy \( p \neq p^r \), then the \( p^r \)-females have a strictly higher fitness in this mixed population than do the mutant \( p \)-females. Further, this holds for any non-zero fraction of invading mutant females. We can show the following results (electronic supplementary material, appendix 2). First, there are no pure strategy equilibria such as the delta function solution given in the fixed benefit case. To see this, suppose that females use a pure strategy; that is, all females in the population mate only with males who have a particular trait value \( z^* \). In this case, any such mate will be totally depleted, and hence the expected payoff to each female will be zero (since from above, \( s(z^*,q) \rightarrow 0 \) as \( q \rightarrow \infty \)). However, a mutant female who will mate with a male of trait value \( z \neq z^* \) will obtain the positive payoff \( s(z,0) \). This shows that mating only with \( z^* \)-males cannot be an equilibrium strategy.

Second, there is a unique equilibrium female preference function \( p^r(z) \), which is an ESS in the above sense. This function is continuous on \([a,b]\), and there is a threshold trait value \( c \) with \( a \leq c < b \), such that \( s(z,p^r(z)) = w^* \) (a non-zero constant) for \( c \leq z \leq b \) while \( p^r(z) = 0 \) and \( s(z,p^r(z)) = s(z,0) < w^* \) for \( z < c \) (applicable only if \( c > a \)). Finally, for all \( z \in [c,b] \), \( p^r(z) \) is monotonically increasing.

In nature, then, this means that males with larger trait values, who would give larger fertility benefits if female preference were uniform, will get more matings than those with smaller ornaments, but they will not have a monopoly on matings. Instead, expected number of matings will decline as ornament size decreases. It may be that all males achieve some matings (so that the threshold value \( c = a \)), or it may be that some threshold is reached, below which males will receive no (consensual) matings at all (so that the threshold value \( c > a \)). Interestingly, given a choice between a male with a higher and a male with a lower trait value, females will not always choose to mate with the bearer of the higher trait. Rather, there will be some probability of choosing each, with more females choosing the bearer of the higher trait value, who will therefore obtain more matings overall, but some choosing the bearer of the lower trait value, who will receive fewer matings overall. This is because the higher trait value male will obtain more matings and hence will be subject to greater sperm depletion relative to the lower trait value male. In effect, the female is negotiating a trade-off between a more attractive, but more depleted male, against a less attractive, but less depleted male. The equilibrium female preferences would be expected to result in the expected benefit from a mating with each male being identical (figure 3).

An intuitive explanation as to why this is follows: for a mathematical proof see electronic supplementary material, appendix 2. Suppose the popularity function \( p(z) \) gave a resulting benefit function \( s(z,p(z)) \) so that some trait value \( z \) delivers a higher benefit than any other trait value. Then females that prioritized matings with \( z \)-males would gain larger benefits, and so any mutant preference function \( p \) that led to more matings with \( z \)-males would be able to invade. The only preference function that cannot be invaded in this way is the one that results in all males giving equal benefit to females who mate with them. Note, though, that more attractive males will still get more matings than less attractive males (figure 3).
benefits [30]. We propose another way to characterize the benefits females obtain from mate choice, in terms of whether they are ‘dilutable’ or ‘fixed’. As we have shown in the model above, this distinction will affect female preference. If females are selecting for fixed benefits, they should only mate with males who provide them with the largest payoff, rejecting all others. On the other hand, if females are selecting for dilutable benefits, their mating pattern will follow a probability distribution so that the best males (those with the highest trait values) get more matings, but do not have a monopoly.

We have modelled explicitly for the cases of good genes (fixed) and fertility benefits (dilutable), but our model could equally apply to other hypotheses for female mate choice, as we now consider. Most types of indirect benefits will be fixed, as characteristics inherited genetically will benefit offspring from all matings equally. This logic applies both for benefits to viability and attractiveness. Where genetic benefits arise from genetic compatibility, they are contingent on complementarity between the parents and so will not flow equally to all females. But they are not dilutable, as the gain of one female is independent of others’ choices (in this case, each female’s optimal preference function would be different, but would correspond to that for a fixed benefit).

Generally, direct benefits will be dilutable. Parenting ability, for example, seems likely to decrease in most cases as the number of offspring with different mothers increases (see the polygyny threshold model [31,32]; although there can be benefits to polygyny too [32,33]). However, there are many exceptions where direct benefits are likely to be fixed. A possible example could be where females choose mates for good parenting, and form socially monogamous pairs. Then paternal care is not diluted, as the male only provides care for his social partner’s offspring. Even if the father sires offspring through extra-pair copulations, the benefits he provides are likely to be fixed to first order; unless the time he spends seeking extra-pair matings impedes his provision of parental care [34]. Another example is the case of prey items acting as nuptial gifts. Then the benefit is direct, but it is not dilutable, as it is consumed entirely by a single female. Nuptial gifts such as spermatophores may be somewhat dilutable, however, if the male’s ability to produce a large spermatophore is affected by frequent copulation.

The different potential benefits to female choice are not mutually exclusive, so evolution will favour combinations of dilutable and fixed benefits. A hypothetical example is a species where females select males for their size and strength, because large, strong males can defend better territory. In this instance, the benefit to females is direct, as they gain better territory, and dilutable since sharing the male with other females means each female gets a smaller share of the rewards from the territory. However, if the male’s size and strength are genetic, the females will also gain fixed, indirect benefits through her offspring inheriting their father’s genetic quality. This model shows that female mate choice can itself offer some clues as to the relative strength of the forces underlying its evolution.

A simple way of combining these two scenarios would be to define the benefit function as a sum of dilutable and fixed benefits, so that \( s(z, p) = \alpha_1 z + \beta_1 p \), where \( \alpha_1 \) and \( \beta_1 \) are constants, \( s_1(z) \); represents the fixed benefits a female obtains from mating with a male of trait value \( z \), and \( s_2(z, p) \); those that are dilutable. As the overall benefit function \( s(z, p) \) is dilutable, female preference will evolve so that the (overall) benefit from any male is the same (with the exclusion of males that fall below a quality threshold). The relative importance of dilutable to fixed benefits could be estimated from the pattern of female choice by looking at mating skew: where fixed benefits are more important, we predict that there will be larger skew, as males offering the optimal fixed benefits achieve most of the matings (though there are other factors that may also affect mating skew; for reviews see [35–37]).

Of course, our model makes a number of simplifying assumptions, and in reality, female choice is likely to be a much more complicated affair. For example, we assume that females are able to accurately assess and compare all potential mates, having no time constraints or costs of mate choice. This is unlikely to be the case, and indeed the time taken to make a decision may itself be costly [38]. If females are not time-constrained, the ability to compare a large number of potential mates may be beyond the cognitive abilities of many species. Even if females have a limited selection of males from which to choose, qualitatively similar results will be obtained, although the evolutionary dynamics will be slower (initial simulation results). This is something we intend to investigate further in future work.

Different preference functions may also have different associated costs, or females may accept males of certain trait sizes with conditional probability based on time and cost constraints [39,40]. We chose not to assess the effects of cost of choice (other than by constraining the set from which the choice is made). While we of course accept that such costs would affect the evolution of mate choice, these effects will depend to a large degree on the nature and size of the costs. This is certainly an important area for future investigations, but in this paper we have aimed to analyse the effects of fixed and dilutable benefits upon mate choice in an idealized setting, and this is more simply and clearly done without considering the many different ways in which a cost could be applied to choice. Nevertheless, it is certainly the case that a non-uniform distribution of costs of mating with different males can potentially moderate the all-or-nothing conclusion that it is always optimal to mate with the ‘best’ males in the fixed benefits case.

In addition, we assume that there is a reliable link between ornament and benefit. This will be justified in cases where the trait has a functional role in determining the benefits females will receive. If the benefit is number of sperm, for example, then testes size could be such an indicator. It can also be justified by recourse to the handicap principle in which male investment in the ornament is correlated with the traits which determine the benefits females receive because of condition-dependent costs [41]. The phenotype-limited fertility hypothesis suggests that females choose males based on their fertilizing ability [5]; for this to be possible, females must be able to assess the fertilizing abilities of males using some trait or combination of traits. We simply assume for simplicity that such assessments are reliable, in the sense that paying attention to the trait value achieves, on average, greater benefits for the female than not paying attention. The effect of signal
unreliability is worth investigating in the future; we expect that it will slow down the evolution of preference functions of the predicted type, but that qualitatively, the results will be the same. However, in this paper we are concerned only with exploring the effects of the conceptual difference between fixed and dilutable benefits, and for this our simplifying assumptions are sufficient.

Something else we have not addressed is the possibility of polyandry, where females mate with more than one male within a breeding season. This could come about in either fixed or dilutable benefits cases if constraints mean that the females cannot achieve the optimal choice. In the fixed benefit case, a female selecting the best male available to her at a given time may later come across better males and thus wish to ‘trade up’. In the dilutable benefit case, the same could occur if females are constrained so that the resultant benefit function is not one that means all males give the same benefits. However, as extra-pair copulations would themselves cause further dilution of the benefits provided by males, this may be less likely.

Once we accept that benefits accruing to a female from a given male can depend on the number of other females he mates with, there is also the possibility that the more mates a male has, the higher the expected benefit to each: the opposite of the dilutable benefits scenario considered here. In some species, it is thought that increased polygyny may in fact benefit females. For example, in birds, breeding in the same territory as increased polygyny may in fact benefit females. For considered here. In some species, it is thought that increased polygyny may in fact benefit females. For example, in birds, breeding in the same territory as other females may decrease the chances of nest predation [32]. This could be modelled by considering a benefit function \( s(z,q) \) that is increasing with increasing popularity \( q \), rather than decreasing as we have assumed in this paper. Although we have chosen not to consider this case here, note that under these circumstances, the ESS strategy could be one where all females will choose males of the same trait value \( x \), if \( s(x,q(x)) < s(x,q(x)) \) for all \( z \neq x \) and delta functions \( q \), and \( q \). However, the exact solution is likely to be highly dependent upon the way \( s(z,q) \) varies with \( z \), giving several possibilities.

A female who mates with a male bearing a trait value preferred by other females in the population may gain some benefit by having ‘sexy sons’ [11,42]. This could be covered by the last framework, with the benefit accruing to a female for mating with a male of a given trait value increasing if more females in the population have a preference for that value. It is therefore interesting to note the similarity of the result in this case (that all females have the same preference) to Fisher’s runaway process. It is also notable that female choice for dilutable benefits in our formulation gives a similar result to the polygyny threshold model [2,31,32], with females balancing the trade-off between attractiveness and sperm depletion, so as to make the expected benefit from each (acceptable) male identical. If the benefit function \( s(x,p) \) declines linearly with increasing \( p \), the resulting preference function will resemble an ideal-free distribution, with males’ popularity being proportional to \( s(x,0) \), which could be seen as the total amount of resources they have to give to females. Thus, although our formalism is simple and intuitive, it encompasses a wide spectrum of possible patterns of female choice, and uncovers previously unrealized relationships between them. While it is not intended to replace the old direct/indirect benefits distinction, it does provide an additional way of considering the evolution of female choice, which could be of use in stimulating new empirical studies that will hopefully unravel the complexity surrounding this area of evolutionary theory.

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REFERENCES


