



# Selection for male stamina can help explain costly displays with cost-minimizing female choice

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## Abstract

In many species, male lifespan is shorter than that of females, often attributed to sexual selection favouring costly expression of traits preferred by females. Coevolutionary models of female preferences and male traits predict that males can be selected to have such life histories; however, this typically requires that females also pay some costs to express their preferences. Here we show that this problem diminishes when we link coevolutionary models of costly mate choice with the idea of stamina. In our model, the most successful males are those who can combine high attendance time on a lek — or, more generally, tenacious effort in their display time budgets — with high viability such that they are not too strongly compromised in terms of lifespan. We find that an opportunistic female strategy, that minimizes its costs by mating with highly visible (displaying) males, often beats other alternatives. It typically resists invasion attempts of genotypes that mate randomly in the population genetic sense, as well as invasion of stricter ways of being choosy (which are potentially costly if choice requires e.g. active rejection of all males who do not presently display, or risky travel to lekking sites). Our model can produce a wide range of male time budgets (display vs. self-maintenance). This includes cases of alternative mating tactics where males in good condition spend much time displaying, while those in poor condition never display yet, importantly, gain some mating success due to females not engaging in rejection behaviours should these be very costly to express.

## Significance statement

In many species, males spend much time and energy on displaying to attract females, but it is not always clear what females gain from paying attention to male displays. The tradition in mathematical models attempting to understand the situation is to assume that random mating is the least costly option for females. However, random mating in the population genetic sense requires females to behave in a manner that equalizes mating success between displaying and non-displaying males, and here we point out that this is biologically unlikely. Opportunistically mating females can cause males to spend much of their time budgets displaying and will shorten male lifespans in a quality-dependent manner.

**Keywords** Female choice · Lek paradox · Preference-trait coevolution · Lifespan evolution · Sex differences

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## Introduction

Can females that show preferences for specific males gain indirect fitness benefits? This idea is fraught with difficulties (Achorn and Rosenthal 2020), with a history of modelling showing that choice evolution is difficult because benefits of purely genetic nature are predicted to be minor, and because persistent choice itself is predicted to favour males with specific genotypes (Charlesworth 1987; Kirkpatrick and Ryan 1991; Van Homrigh et al. 2007; review: Kokko et al. 2003). If these genotypes are so prevalent that picking a random male is unlikely to be greatly inferior to one that is the result of female choice, then a randomly mating female is at an

advantage: she avoids paying the direct costs of mate choice, without compromising mate quality much at all. This is the essence of the lek paradox: strong directional selection on male traits should make choosy behaviour unnecessary to find males who possess the desired traits, and in the (near) absence of benefits of choice, even mild costs of choice, e.g. the small risks taken by females when travelling to a lek, should be sufficient to make choice selected against and vanish (Borgia 1979; Pomiankowski 1987; Kirkpatrick and Ryan 1991; Kirkpatrick and Barton 1997).

There are numerous proposed solutions to the lek paradox (review: Radwan 2008), many of them focusing on the ways that variation in male ‘quality’ can be maintained. The genic-capture hypothesis states that males signal as a function of their condition, which in turn is determined by very many loci, making condition a large target for mutations (Rowe and Houle 1996; Parker and Garant 2004; Tomkins et al. 2004; Dugand et al. 2019). Other suggestions include mutations being predominantly deleterious (Iwasa et al. 1991; Tomkins et al. 2010; Mallet et al. 2012), sexual selection itself elevating mutation rates (Bartosch-Härlid et al. 2003; Petrie and Roberts 2007), preferences for mates with high genome-wide heterozygosity (Fromhage et al. 2009), nongenetic inheritance (Bonduriansky and Day 2013), non-additive genetic benefits (Neff and Pitcher 2009), interactions between direct and indirect fitness benefits (Dhole et al. 2018), and genotype-by-environment interactions (GEIs) (Rodriguez and Greenfield 2003; Kokko and Heubel 2008; Greenfield et al. 2012; Miller and Svensson 2014) that generalize to spatial mosaics with local adaptation that combines with gene flow (Holman and Kokko 2014), and sexual conflict counteracting the depletion caused by female choice (Hall et al. 2010; Zajitschek and Connallon 2018). As a whole, costly female choice can be maintained in models, but a typical finding is that costs must remain very small as the process maintaining variation in heritable differences in male ‘quality’ is not expected to yield large differences in mate value (in the absence of direct benefits to choice).

The lek paradox is tricky to quantify empirically because it is conceivable that female preferences that can cause strong selection on males may be very cheap for the female to express, creating a task where minute costs should be contrasted with minute benefits (Kokko et al. 2003; see also Sharma et al. 2010). Selection on male traits exists even if females are ‘passively’ attracted to signalling males, simply to ensure that fertilization takes place at an appropriate time; a stronger signal emitted by a male leads to more females finding that male (Parker 1983). More recently, it has been pointed out that a focus on fixed costs of choosiness may be an unrealistic assumption in mate choice models (Kokko et al. 2015). In reality, should most males satisfy currently evolved female criteria, females may accept the first (or one of the first) male encountered, and this diminishes choice

costs at roughly the same pace as the preferred male phenotype becomes common, potentially stabilizing a coevolutionary outcome where males signal and females choose signalling males.

Here we point out another angle to the cost question — one that has been discussed empirically (mainly from the male side), but rarely modelled. Empirically, there are numerous studies showing that attendance time on a lek (Apollonio et al. 1989; Hill 1991; Dyson et al. 1992; Fiske et al. 1998; Friedl and Klump 2005), or more generally time spent displaying (in non-lekking species, Dearborn et al. 2005; Poesel et al. 2006; Souza et al. 2021), can explain a substantial part of male mating success. If male condition determines how much of his time budget he can spend displaying (which is energetically costly per se and also diminishes time spent on self-maintenance), then for females, mating with any male who is currently displaying appears to be a relatively cheap way to assess male quality. In short, being present on a lek combines measuring lekking effort and longevity (Kokko et al. 1999) — an idea that we capture with the term ‘stamina’, which we measure in our model as the total time a male spends displaying.

With our model, we aim to fill in a gap in theoretical literature. The idea that the temporal aspect of male displays may convey information to females has been modelled before, but not very extensively: Castellano (2009) considered competition between one high-quality male and one low-quality male who evolve to differ in the probabilities that they are present at a breeding site on any given night (where the choice of night as the relevant display time stems from Castellano’s chosen taxon, treefrogs). Not displaying is safer in his model as falling victim to predation occurs (probabilistically) while displaying. Females in his model vary in how much effort they spend investigating male displays (Castellano 2009), but this variation is not associated with costs paid by females, and the actual evolutionary response of females is not tracked. Costs of choice are, in other models, known to change the evolutionary dynamics even if they are small (review: Kokko et al. 2006, newer work: Etienne et al. 2014; Kokko et al. 2015; Dechaume-Moncharmont et al. 2016). Female-male coevolutionary models, however, rarely derive male lifespan explicitly (they often tacitly or explicitly assume discrete generations), and the structure of these models typically does not allow making statements about male time budgets — thus the components of stamina (proportion of time spent displaying, and male lifespan) are typically not examined.

As a whole, therefore, the link between ‘stamina’ and the general theory of costly female choice (Kokko et al. 2006; Radwan 2008) remains unexplored to this day. By combining a budget approach to variable lifespans of males and females, our model shows that theory building has for all too long forgotten about a simple principle highlighted by

early work on mate choice (Parker 1983; Wiley and Poston 1996): female behaviour can be largely driven by cost minimization, but since cost minimization does not equate with random mating in the population genetic sense, this does not compromise the ability of female behaviours to cause strong selection on male display traits.

In our model, we intentionally deviate from a traditional assumption in female choice models that random mating is the least costly option for females. Male displays typically involve signals that make a male very visible (or detectable via another sensory mode) to females. Random mating in the population genetic sense means that mating pairs form in proportion to genotype presence in the population. To achieve random mating when some males are highly visible while others are not, females would have to behave in ways that counteract the visibility inequality among males. Our model includes such females (we call these R females as they achieve truly random mating), not because we expect them to be found in nature, but because their presence is the default in models that have cost-free random mating as a baseline assumption. While we assume R females pay some costs, these may be larger or smaller than the costs paid by D females, who we assume to only mate with displaying males. The costs of both strategies are elevated with respect to the least costly strategy, denoted O for opportunistic behaviour, where females are attracted to male signals ('passive attraction' sensu Parker 1983) as this speeds up mate-finding, but they also accept non-displayers, should such a male be encountered first.

Opportunism in our terminology refers to a cost-minimizing behaviour: females mate with whoever they first found to fertilize their eggs. To be precise, an opportunistic female's propensity to mate with each displaying male is  $\alpha$  times their propensity to mate with each non-displaying male (the latter is assigned the value 1; we assume  $\alpha > 1$  measures the relative visibility of displaying males). Here,  $\alpha$  simply measures how well display elevates the 'detectability' of the male. Our 'opportunistic strategy' is a type of indirect choice sensu Wiley and Poston (1996), or a 'mating bias' sensu Kokko et al. (2003). Because opportunistic females accept the first encountered conspecific, we assign O strategy the lowest cost and contrast it with costs that R or D females pay. This also captures the gist of Parker (1983)'s ideas about passive attraction, though we note that 'passive' should not necessarily be equated with 'immobile' but more broadly with speed and efficiency of mate-searching. The latter two costs can of course be unequal, and we do not make a priori claims which one is the larger one. Our model produces predictions regarding male stamina, in that it predicts both time spent displaying and the lifespan consequences of it, together with the consequences for female choice strategies (R, D, or O) that will prevail.

## Model

Our model tracks the evolution of three types of female genotypes in a population where each individual is haploid, with two loci. A 'quality' locus (with alleles Q and q) impacts viability in both sexes: q individuals suffer higher mortality than Q individuals. Both sexes have their mortality elevated by a factor  $\beta > 1$  if their genotype is q. Male mortality is additionally increased as a result of displaying. Displaying causes additional mortality for both male types, but does so more strongly for q than for Q males, a difference that we capture with  $\gamma_q > \gamma_Q$ . We assume that males possess a reaction norm that links quality (q or Q) to the time budget (time spent displaying) as detailed below. The second locus, which modifies female preferences, is only expressed in females, and it has three alternative alleles R, D, and O.

We deviate from typical population genetic assumptions which assume discrete generations, and we instead allow individuals to vary in their lifespan by modelling a continuous mortality rate impacting them throughout life. Baseline mortality is  $\mu_0$  for Q individuals and  $\mu_0\beta$  for q individuals ( $\beta > 1$ ), which in a continuous-time setting yields expected lifespan of  $\mu_0^{-1}$  and  $(\mu_0\beta)^{-1}$ , respectively. Note that a continuous mortality hazard, with an exponentially distributed lifespan, can take any positive value, including values  $> 1$ . For example, if one time unit is defined as one year, and mortality is  $\mu_0 = 12$ , this means an average life lasts 1/12 years, i.e. one month. For our examples, we use  $\mu_0 = 1$ , which scales the time units such that a non-displaying Q male has a lifespan expectation of 1 unit of time (during which breeding can occur continually); realized lifespans will be exponentially distributed such that some die before and some after reaching 1 unit of age.

In females, lifespan is additionally impacted by their preference alleles, which we denote O, R, and D for opportunistically and randomly mating females as well as the display-preferring females, respectively (these obviously also impact the mating dynamics, which we describe in detail below). We assume that O females achieve mating in the least costly way: they are more likely to mate with (currently) displaying males than with (currently) non-displaying males, but do not reject non-displayers either should they encounter them. O females thus avoid any costs of actively rejecting a male or looking for them for longer than minimally necessary. Since their choice is based on ease of detecting males, their mortality remains at the baseline of unavoidable mortality, i.e.  $\mu_0$  or  $\mu_0\beta$  depending on their quality (Q or q).

R females mate with males in proportion to male genotypes in the population. This implies random mating, which traditionally is assumed to be cost-minimizing for females. As outlined above in the 'Introduction', we argue that such

**Table 1** List of parameters used in the model. Value range indicates the range from which each parameter is assigned a value for, independently for each simulation run and logarithmically scaled for all values except  $\alpha$ . The mutation ranges were chosen based on estima-

tions of single base substitutions, average genome size, and known offspring-parents genomic comparisons (Keightley et al. 2014a, b for insects; Koch et al. 2019 for mammals; Lynch 2010 for humans)

Symbol	Description	Value range
$\alpha$	Enhancement of visibility (detectability) of displaying males	1...5
$C_R$	Choice cost paid by R females	$10^{-6} \dots 10^{-2}$
$C_D$	Choice cost paid by D females	$10^{-6} \dots 10^{-2}$
$\nu$	Mutation rate. Determines transition from Q to q	$10^{-5} \dots 10^{-1.5}$
$\mu_0$	Baseline mortality applied to every individual in the population	1
$\beta$	Additional cost increasing mortality of q males irrespective of their time budgets	$10^{-2} \dots 2$
$\gamma$	Cost paid by displaying males. Depends on the quality allele ( $\gamma_q > \gamma_Q$ ). Two values are generated for each run; the smaller one is assigned as $\gamma_Q$ , the larger one as $\gamma_q$	$10^{-2} \dots 10^1$

an assumption ignores the ease with which displaying males are found by female. If some males display and others do not, achieving random mating requires females to effectively increase their mate-searching effort to locate non-displaying males at an equivalent rate as they do displaying males. While this could be seen to make completely random mating a priori unlikely, we nevertheless include it as an evolvable option in our model, but deviate from the tradition of population genetic models that assume it to be the least costly option. Therefore, compared with O females, R females' mortality is somewhat elevated: we multiply the relevant baseline ( $\mu_0$  or  $\mu_0\beta$ ) with a factor  $1 + C_R$  where the cost  $C_R > 0$  (see Table 1 for the value range), yielding mortalities  $(1 + C_R)\mu_0$  or  $(1 + C_R)\mu_0\beta$  depending on female quality (Q or q).

Finally, females with the D allele mate with displaying males only, and ignore non-displayers even if they are encountered. We form mortalities of D females similarly to above, such that mortalities become  $(1 + C_D)\mu_0$  or  $(1 + C_D)\mu_0\beta$  for Q or q females, respectively. It is a priori not clear if  $C_D > C_R$  or vice versa, as D females may pay costs such as having to ignore the first available male should an encounter be with a non-displayer, perform costly avoidance behaviour should such males behave harassingly, and possibly having to travel further to find displayers. The magnitude of such costs may be very system-dependent, and we thus consider a variety of costs and their relative ranking.

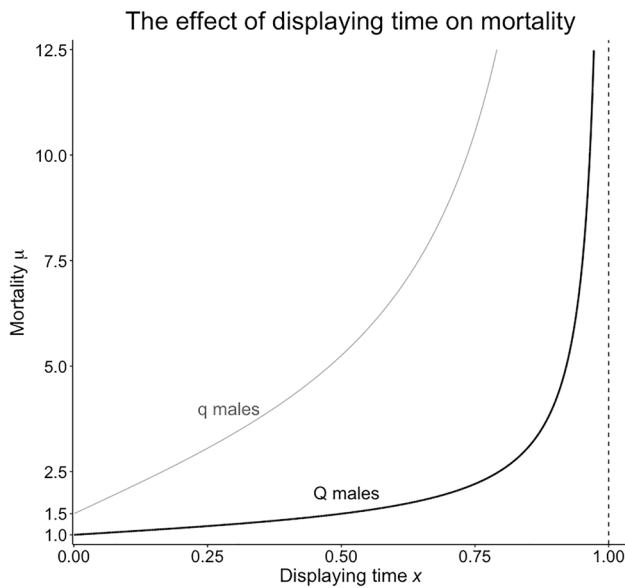
Note that it is unlikely that either  $C_R$  or  $C_D$  take large values, as all females are assumed to have relatively little trouble locating a mate. Even so, the sensitivity of published mate choice models to small costs of choice (Kirkpatrick and Ryan 1991; Pomiankowski et al. 1991) creates an a priori expectation that mild costs can make

the difference between presence and absence of choosy behaviour at evolutionary endpoints; thus, values close to 0, but positive, will be of interest here.

In order to maintain variation in quality, we assume that there is a mutation rate  $\nu$  (see Table 1 for the exact value range) from Q to q without any back mutation. Our model is in line with the 'biased mutation' approach of e.g. Iwasa et al. 1991 and follows the gist of genic capture: mutations on one 'quality' locus approximate the many low-rate mutations on a large number of loci which all contribute to a male's condition (Rowe and Houle 1996). At the same time, we do not model mutations between O, D, and R preference alleles; instead, we initiate populations with one predominant preference genotype and see if a rare competing genotype can spread.

### Male time budgets

Males spend a proportion ( $0 \leq x \leq 1$ ) of their time displaying (without making any assumptions of whether they do so in an aggregated manner or not). Displaying is costly to males, as time spent displaying prevents activities related to self-maintenance such as foraging, resting, and hiding from predation. These costs are quality-dependent: displaying increases mortality of Q males to  $\mu_Q = \mu_0 (1 + g(\gamma_Q, x_Q))$ , where  $x_Q$  ( $0 \leq x_Q \leq 1$ ) is the proportion of time spent displaying, and  $g()$  denotes a function that specifies how strongly mortality increases with the proportion of a male's time budget that is spent displaying. For q males, the equivalent expression is  $\mu_q = \mu_0\beta (1 + g(\gamma_q, x_q))$ . We run our main analysis assuming  $g(\gamma, x) = \gamma \tan(\pi x/2)$  (see SI 1 for more details), which creates positive finite mortalities for all  $0 \leq x < 1$ , increases with  $x$ , and becomes infinite (i.e. creates zero lifespan,  $L=0$ ) when the male has no time left for



**Fig. 1** Mortality assumption (effect of displaying time  $x$  on mortality  $\mu$  of males) of our main model, exemplified with  $\mu_0 = 1$ ,  $\beta = 1.5$ ,  $\gamma_Q = 0.5$ ,  $\gamma_q = 2.5$ . The low-quality male  $q$  has a higher baseline (intercept at  $\beta\mu_0$ , light grey) than the high-quality male  $Q$  (black bold line). The vertical dashed line is the maximum display time budget  $x = 1$  that, if adopted, would lead to infinite mortality, i.e. zero lifespan

self-maintenance at all, at  $x = 1$  (Fig. 1). We consider zero lifespan at  $x = 1$  a biologically plausible property, though we note that there are species where males do not feed after reaching maturity and devote all their time to mate-searching and mating, dying shortly thereafter (e.g. *Achroia grisella*, Soulsbury 2019; *Clunio marinus*, Kaiser et al. 2021, though it is also a species with little female choice). For this reason, we also ran our model with the alternative assumptions  $g(\gamma, x) = \gamma x^2$  and also  $g(\gamma, x) = \gamma x$ . Using either of these functions makes  $x = 1$  produce finite mortalities and thus permits some lifespan for males who invest nothing in self-maintenance. This model variant gives qualitatively similar results (we comment on the differences where relevant). In both model variants, we assume  $\gamma_q > \gamma_Q > 1$ , so that the display-induced increase in mortality is steeper for low-quality males.

Stamina combines both lekking effort, described as a displaying time  $x$ , and longevity of a male, which we denote as  $L$ . Thus, a lifetime measure of stamina is  $S = xL$ . Displaying time  $x$  affects mortality (positively, since all our choices for the function  $g(\gamma, x)$  increase with  $x$ ) and, consequently, lifespan (negatively). Lifespan  $L$  is the inverse of mortality, thus  $L = \frac{1}{\mu(1+g(\gamma, x))}$  and  $S = \frac{x}{\mu(1+g(\gamma, x))}$ .

While displaying is costly, it also makes males easier to spot by females, which elevates male mating success if at least some females are  $O$  or  $D$ . We assume that displaying males are more visible by a factor  $\alpha > 1$ .

We assume a reaction norm such that  $Q$  males use a different time budget for displaying than  $q$  males. We do not, however, model the reaction norm genetically. Instead, we derive the optimal values for  $x_Q$  and  $x_q$  when the population currently consists of any mix of  $O$ ,  $R$ , and  $D$  females. Whether males have evolved to use the optimal reaction norm (i.e. the two optimal values  $x_Q$  and  $x_q$ ) is an open question: it depends on the rate of evolution of this reaction norm compared with the rate of evolutionary dynamics of the two loci we model explicitly. To span the entire range of possibilities, we model two scenarios, labelled 0 (male reaction norms evolve much more slowly than the dynamics of preferences and qualities) and 1 (reaction norms evolve very fast). In scenario 0, we begin with a population where one female preference allele predominates, and assume that the male  $x_Q$  and  $x_q$  values are adapted to that preference over a prolonged evolutionary time, and fail to undergo any change when, as a result of an alternative female preference allele being introduced, the frequencies of the  $q$  and  $Q$  alleles begin to change. In scenario 1, reaction norm evolution is assumed so fast that males (both  $Q$  and  $q$ ) always use optimal time budgets for the current mix of female preferences in the population (the solutions are provided in Supplementary Information SI 1). Real-life situations are probably somewhere between 0 and 1.

## Dynamics

We track the number of all six possible genotypes for females (denoted  $F$  with appropriate subscripts, e.g.  $F_{QO}$ ) as well as males (denoted  $M$ , e.g.  $M_{qD}$ ) over continuous time, which we in practice discretize into steps of length  $dt$ . Note that despite us assuming a 1:1 primary sex ratio, the equilibrium numbers of living females of a particular genotype can differ from those of males of the same genotype, because mortalities that act over the entire lifetime can differ between the sexes (SI 2) and impact how long an individual stays in the pool of living individuals.

We initiate populations with only one of the three preference alleles present, and let the population find its equilibrium frequency for the  $Q$  and  $q$  alleles, assuming that males are adapted to the preference allele present (see SI 1 for the computation of male time budgets). Thereafter, we introduce an alternative preference allele at frequency 0.01, and track the dynamics for 1000 further time units, until there is no further change in genotype frequencies. Depending on scenario (0 or 1), the reaction norm of male time budgets (the values of  $x_q$  and  $x_Q$ ) is kept at the initial values or updated to match the current genotypic composition of the female population throughout the computation.

We assume that the population is regulated through recruitment. Each small time step (of length  $dt$ ) is associated with deaths that also create vacancies that, in turn, are filled with recruiting new individuals produced by the population. The vacancies are the pooled result of existing adults dying at their appropriate death rates; e.g., low-quality R females contribute  $F_{qR}(1 + C_R)\mu_0\beta dt$  vacancies through their deaths. The total number of vacancies is the sum of all 12 different categories of deaths (SI 3). All living females mate at the same rate (reflecting our assumption that costs of choice increase female mortality, rather than increasing difficulties securing a mate or other problems with fecundity; dead females are simply not available as mothers, SI 5); thus, each female that is alive is equally able to contribute offspring to filling vacancies. It follows that maternally inherited genotypes simply reflect the proportion of mothers alive in the population at time  $t$ .

The sires are chosen according to female genotype: for R females, the proportion of different sires is equal to the proportion of males (6 genotypes) in the population at time  $t$ , and  $j$  indicating one of the preference alleles (likewise for  $k$  which denotes competing males' preference alleles). For O females, these proportions are adjusted such that the relative frequency of displaying males as sires is elevated by a factor  $\alpha$ : a male of quality  $y$  (either Q or q) and preference allele  $j$  is the chosen sire with probability

$$m_{yj}(t) = \frac{M_{yj}(t)}{\sum_{k=\{D,R,O\}} M_{qk}(t) + \sum_{k=\{D,R,O\}} M_{Qk}(t)}, \text{ i.e. where } y \text{ indicating either Q or q,}$$

and  $j$  indicating one of the preference alleles (likewise for  $k$  which denotes competing males' preference alleles). For O females, these proportions are adjusted such that the relative frequency of displaying males as sires is elevated by a factor  $\alpha$ : a male of quality  $y$  (either Q or q) and preference allele  $j$  is the chosen sire with probability

$$\frac{\alpha M_{yj}(t)x_y + M_{yj}(t)(1 - x_y)}{\sum_{k=\{D,R,O\}} (\alpha M_{qk}(t)x_q + M_{qk}(t)(1 - x_q)) + \sum_{k=\{D,R,O\}} (\alpha M_{Qk}(t)x_Q + M_{Qk}(t)(1 - x_Q))}$$

Finally, for D females, only displaying males have positive probabilities of being the sire; these females have sires according to probabilities

$$\frac{M_{yj}(t)x_y}{\sum_{k=\{D,R,O\}} M_{qk}(t)x_q + \sum_{k=\{D,R,O\}} M_{Qk}(t)x_Q}$$

Since the above probabilities are somewhat unwieldy due to different male genotypes all offering both displaying and non-displaying males at any point in time, and because each mating can yield up to 8 different kinds of offspring (up to 4 genotypes depending on mother's and sire's genotype at the two loci, with the offspring additionally categorized as male or female assuming 1:1 sex ratio), updating the state of the population from  $t$  to  $t + dt$  requires tracking a large set of frequencies of offspring filling the total vacancies via different mother and father combinations (SI 4–6). This means that we track it numerically (note that we assume no stochasticity and can create deterministic predictions, even if we do not provide analytical solutions).

## Results

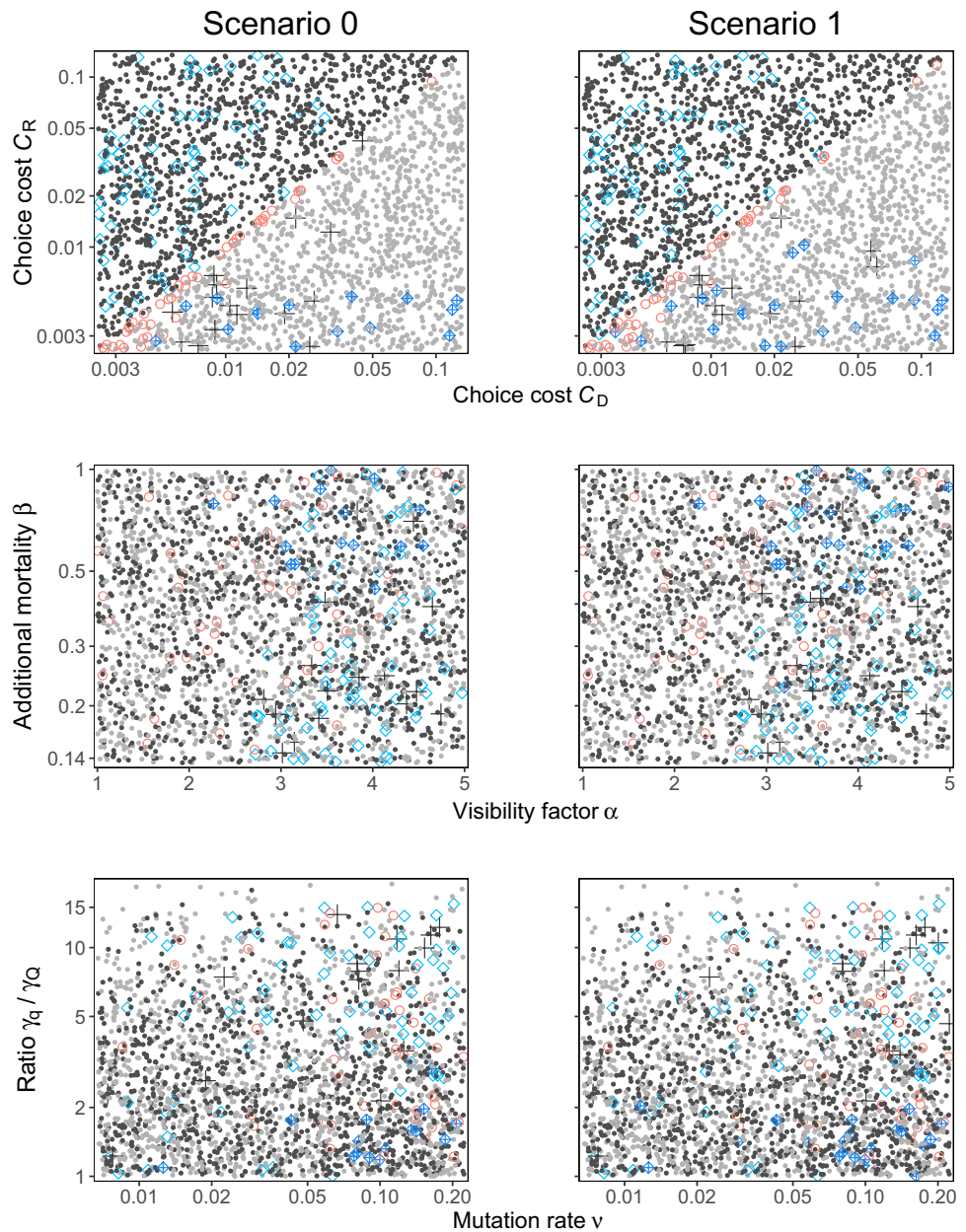
In initial trials, running the model with biologically plausible parameter values almost always indicated that if opportunistically displaying O females are presently fixed in the population, an invading alternative genotype (R or D) will not spread from rare. This is true whether we consider scenario 0 (where male display time budgets do not change when female genotypes change) or 1 (where males change immediately to reflect current female genotypic composition). However, the stability of O does not necessarily prevent other genotypes being similarly stable if they (instead of O) are initially fixed. To find an overview over the numerically complicated situation, we chose 2500 random combinations of parameter values  $\alpha$ ,  $\beta$ ,  $\gamma_q$ ,  $\gamma_Q$ ,  $\mu_0$ ,  $C_R$ , and  $C_D$  (see SI 7 for the MATLAB code generating mentioned values), and ran each combination  $2 \times 3 \times 2 = 12$  times; this reflects two scenarios (0 or 1), three possibilities for the female genotype that is initially fixed (R, D, or O), and two possibilities for the invading genotype (e.g. R or D if O is initially fixed). The outcome was in each case recorded as the fixed genotype resisting invasion (stable) or being invadable (if the invader was able to increase its frequency from the initial 0.01 invasion).

Taking into account the number of genotypes, there are six unique invasion trials (e.g. O strategy invades a population initially fixed for R; O strategy invades D). This yields  $2^6 = 64$  qualitatively different categories. One example of a hypothetical category is 'R resists invasion by O but cannot resist invasion by D, D resists invasion by O but cannot resist invasion by R, O resists invasion by either R or D' which would be suggestive of multiple equilibria — either a polymorphism between R and D or then O fixed and uninvadable by others. Many of these categories, including the above example, are hypothetical (it is unlikely that O would do so badly in one competitive context but so well in another) and were indeed never found in our trials.

We should note that all the possible 64 categories, in principle, can occur in either scenario 0 or scenario 1, but since these differ in their assumptions about the male evolutionary response, we present the results separately (Fig. 2). In total, we found 10 of the 64 possible categories in our trials, and six of those were found at least 10 times. These six are distributed unequally with respect to at least some of the axes of the multidimensional parameter space (Fig. 2 plots them against different axes of parameters and separately for scenarios 0 and 1; for  $\gamma$ , we plot the categories against the ratio  $\gamma_q/\gamma_Q$ , as this indicates how much more sensitive q males are to display costs).

Scenarios 0 and 1 proved very similar (SI 8), with only very few parameter combinations yielding a category

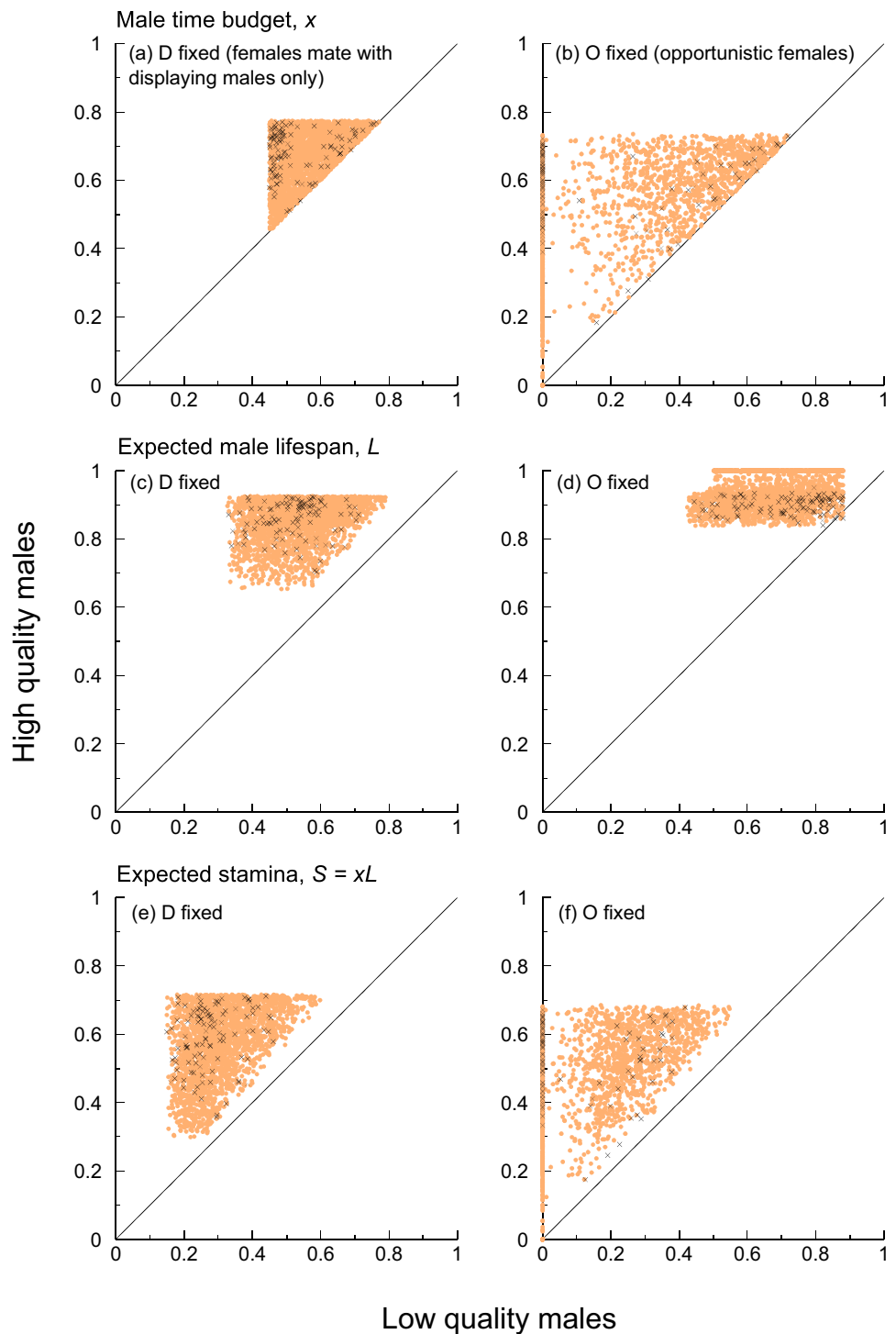
**Fig. 2** Categories found in 2500 parameter combinations, shown whenever a category was found at least 15 times. Each parameter combination was tested twice (left column: scenario 0, right column: scenario 1) yielding near identical plots. The same dots also appear in each of the rows, plotted against different parameters as indicated on the axes; however, for  $\gamma_q$  and  $\gamma_Q$ , we plot solutions against their ratio (which explains the uneven distribution along the y axis). Dots represent cases where O is stable against both D and R. Dark-grey dots — O is stable; D is stable against R but is invaded by O. Light-grey dots — O is stable; R is stable against D but is invaded by O. Red circles — O is stable; D is stable against R and vice versa. Light blue diamonds — O is stable against R; D is stable against R; O invades D and vice versa. Blue crossed diamonds — O is stable against D; R is stable against D; O invades R and vice versa. Black crosses — O is stable against R; R is stable against D; O invades D and vice versa (see more information in SI 8)



(colour/symbol) change between corresponding dots (same parameter combination) in the left and right panels in Fig. 2. The opportunistic female strategy clearly proved its potential to be stable in a very widespread range of parameter combinations; this was the case (i.e. O resists invasion by R as well as by D) in 2400 and 2393 (out of 2500) parameter combinations in scenarios 0 and 1, respectively. In the alternative model formulation where  $g(\gamma, x) = \gamma x^2$ , the corresponding numbers were 2262 and 2260, while in the second alternative model (with  $g(\gamma, x) = \gamma x$ ), these numbers are 2432 and 2366. The clear majority of these cases (marked as light and dark grey dots in Fig. 2) had an additional stability property in that either D is stable against R (if  $C_D < C_R$ ) or vice versa (if  $C_R < C_D$ ), but since neither strategy was stable against

O, we expect O to prevail as a whole. Where  $C_R \approx C_D$  or when both were small and  $C_R < C_D$ , we also found it to be possible that D is stable against R and vice versa (red circles in Fig. 2). This solution features alternative stable equilibria reminiscent of other female choice models involving an invasion barrier (e.g. Kokko et al. 2002) where pre-established random mating makes it difficult for costly choice to invade as males do not display — but maintaining choice (if it somehow became established first) is much easier: now males do display, and a female who fails to express the preference (say, a mutant R female) will produce male offspring with suboptimal mating success. However, the stability of either D or R is only true with respect to each other, and including O as an opportunistic alternative makes it easier

**Fig. 3** Life history consequences of the simulated 2500 parameter combinations assuming that either D (left columns) or O (right columns) is fixed. Solutions are categorized based on whether O is stable against both R and D (orange) or invadable by at least one of them (black). **(a, b)** Whether D or O is currently fixed in a population, high-quality males use more time for displaying than low-quality males. **(c, d)** High-quality males typically also live longer, but the difference is smaller and can in rare cases be reversed if females mate opportunistically. **(e, f)** The expected total time that a male spends displaying (calculated as  $xQ$  or  $xq$  times the expected lifespan) is always higher for Q males than for q males, except if both are zero; this gives support for the idea that choosing a mate among the displaying males makes females mate disproportionately often with Q males



for preferences to spread than assuming that females only mate with displaying males (D).

It is therefore of interest to compare the male traits and their life history consequences of a situation where females express either the D or the O genotype (note that the R genotype will not cause selection for  $x > 0$  and male lifespans will then not be impacted by display effort but only reflect  $\mu_0$  and

$\beta$ ). Whether D or O is fixed, high-quality males display more than low-quality males ( $x_Q > x_q$ , all dots above the diagonal in Fig. 3a,b). When O is fixed, the overall range of possibilities becomes broader: largest display time budgets found are no smaller than when D is fixed, but there are now also solutions where the time spent on display is small, and in many cases it is zero for low-quality males while remaining



positive for high-quality males (dots along the  $y$  axis in Fig. 3b). Here, the model effectively produces alternative mating strategies (Castellano et al. 2009; Bro-Jørgensen 2012) as an emergent property: when  $x_Q > 0$  and  $x_q = 0$ , low-quality males specialize in a low-risk, low-gain strategy of avoiding paying costs of displaying and instead attempt to live as long as possible (maximum self-maintenance) and gain some matings, which is possible due to females not strictly avoiding matings with such males (opportunism, O).

Note that the stability of O is compromised in those cases where  $x_Q > 0$  combines with  $x_q = 0$  (crosses along the  $y$  axis of Fig. 3b,f). Here high-quality males spend relatively little time in a non-displaying state, while low-quality males are overrepresented among the non-displayers. Display therefore, under these conditions, offers a very reliable way to find Q males, and consequently it is worth spending some effort to avoid mating with non-displayers (as D females do, while O females do not).

There are two consequences for male lifespan whenever display-oriented females (D) are replaced by opportunistic females (O). First, lifespans of males become as a whole longer (compare Fig. 3c to Fig. 3d), especially so for low-quality males. Second, although rare, the set of solutions also include cases where the relationship between male quality and lifespan is negative (some dots are below the diagonal in Fig. 3d). This recapitulates a well-known result from ‘good genes’ versus ‘Fisherian’ sexual selection: when males evolve optimal reaction norms for a trade-off between mating success and survival, it is possible that best males benefit so much from intense display effort that their lifespan drops below that of poor-quality males, without this compromising the effect that females benefit when mating with the better males (Kokko 2001; Kokko et al. 2002).

## Discussion

Classic coevolutionary models for female choice and male traits often use preference functions where males possess traits and females mate disproportionately often with males who show above-average trait values (Lande 1981; Kirkpatrick and Ryan 1991; for an empirical evaluation, see McGuigan et al. 2008); evolutionary change is then often modelled from one discrete generation to the next. Our approach differs from this classic set of assumptions: both female and male generations can be overlapping, and males’ time budgets can be split between displaying and self-maintenance. This allows us to make an important point that choosy females may not have to use the strongest ‘levels’ of choosiness — mating strictly with displayers only — to achieve a situation where male quality is detected in a manner that can yield coevolution between female preferences and male traits. In brief, when males make themselves detectable (via

displaying), and this requires behaving in a manner that is difficult to maintain over prolonged periods of time, then males are selected for stamina. Under such conditions, the cost-minimizing behaviour by females — approaching displaying males but also accepting non-displayers should such a male be encountered — can also reduce the chances of mating with suboptimal males. Our model, by considering three different alleles for female choice (random, opportunistic, and strictly display-oriented), shows that opportunistic choosiness by females can be very often stable.

Our results highlight the importance of considering that males do not have strictly zero mating success when they do not display. This has been previously shown to be of crucial importance for predicting the slope of allometric relationships of sexually selected traits (Fromhage and Kokko 2014), and in our model it opens the door for alternative mating strategies (e.g. satellite males, Castellano et al. 2009; or more generally mating outside the lek, Lanctot et al. 1997). It makes it easier to maintain equilibria with female choice and male display traits, while simultaneously extending the time that males following the optimal reaction norm can spend on self-maintenance, which prolongs expected male lifespan. In some of the cases we found, this also means that lifespans become relatively similar across male qualities, while the display efforts simultaneously become more unequal: higher quality males’ superiority is shown in much better ‘stamina’, i.e. longer expected lifetime display effort, which separates male qualities better than lifespan itself is able to do.

Castellano (2009) showed that males differing in quality may show adaptive differences in stamina (‘endurance’ in his terminology), but did not proceed to deriving evolutionary trajectories that predict frequencies of females using plays an important role in selection of males. Our model thus extends a line of thinking that starts from Parker (1983) through Castellano (2009) to show that the same model can produce male displays when females either minimize choice costs or perform more active avoidance of non-displayers (we showed that sometimes females who only mate with displaying males outperform opportunistic females). This can also be seen to provide a mathematical backbone to the work on treefrogs by Friedl and Klump (2005), who proposed that random mating implies, for females, mating with better than average males should ‘randomness’ involve mating with those males who participate in a chorus (an idea akin to passive attraction sensu Parker 1983; see also Botto and Castellano 2016). However, note that their ‘random’ is more akin to our ‘opportunistic’ female strategy, as in our model we strove to maintain the meaning of random mating of many population genetic models where all males (who are alive) have strictly equal mating success.

Terminology aside, our model shows that cost-minimizing behaviour by females may very well be compatible with causing considerable selection on males, including cases where the majority of male lifespan is spent displaying, and male lifespan is significantly shortened from what a male could achieve if he spent all his time budget on self-maintenance (although this shortening is less drastic than if female strictly only mated with displaying males).

Like all models, ours makes certain simplifying assumptions. Many could be relaxed in future work, e.g. that there are discrete genotypes for female behaviour and only two male quality classes. Perhaps more importantly, our model ignored, for simplicity, that the costs paid by a specific strategy may depend on the distribution of males in the population (Kokko et al. 2015). In our context, relaxing this simplification might alter conclusions particularly in the context of the ease with which the opportunistic genotype O replaces random mating if the random mating allele R predominates in the population. The present model often has R unable to resist such an invasion, but this may appear puzzling, since R causes display effort to be zero and the O genotype should not be able to mate any differently from R under such a setting. The reason that O spreads in our model is that we have a priori assumed it to minimize costs while R does not necessarily do so. In the special case where no males display at all, the costs paid by O and R (if any) should be similar; this is a good reason to consider costs as a function of male frequencies and time budgets in future models. We suspect this might make it harder for O to invade from very low frequencies, but it should not impact our main message that O, once established, is very commonly able to resist invasion of alternative genotypes.

Another two simplifications in our model relate to male life histories. We assumed, for simplicity, that male display budgets reflect an abstract ‘quality’ (Hunt et al. 2004), which we conceptualize as condition-dependence that predicts a constant proportion of time spent displaying (as opposed to self-maintenance). The ability of a male to do this was not assumed to depend on age, and we likewise did not consider that displays may show continuous variation from less to more intense (we dichotomized them simply as being temporally ‘on’ or ‘off’), nor did we model the temporal dynamics of foraging that ultimately fuels male mating effort. Life history theory, interestingly, appears to consider the dynamics of resource gains, known as the capital vs. income breeding contrast, mostly from a female perspective (e.g. Houston et al. 2007; Rosenheim et al. 2008; Pélisson et al. 2013; Davis et al. 2016; Culina et al. 2019; Hopkins et al. 2021), but there are equally interesting male questions waiting to be answered (Mysterud et al. 2008; Soulsbury 2019). Thus, future

studies could implement more explicit resource management questions to male–female coevolution studies. This could also be linked with studies on cost mitigation by females not considered by us, e.g. mate choice copying, or mate fidelity.

As a whole, our study provides credence for the idea that female choice can be cheap to express when males not only have to possess certain traits to qualify as mates, but have to spend effort in maintaining a time budget for displaying (Apollonio et al. 1989; Dyson et al. 1992; Fiske et al. 1998; Dearborn et al. 2005; Poesel et al. 2006; Castellano 2009; Souza et al. 2021). The numerous ways to maintain male quality variation may not yield massively large heritable variation, but if females behave opportunistically in the manner outlined by our model, their ability to ‘have their cake and eat it too’, i.e. find a male while also avoiding the poorer subset of males, will cause strong selection on males, create optimal life histories of males with less than maximal self-maintenance, and as a whole help explain why males may evolve shorter lifespans than females.

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**Data availability** Data generated by the model (outcomes from the simulations) are presented in the Supplementary Information. Full list of outcomes of the model is available on zenodo (<https://zenodo.org/record/6434599#.YILety-23BI>).

**Code availability** The MATLAB script file with the model code, script files for Figs. 2 and 3, as well as all the necessary files for model to run are available on zenodo (<https://zenodo.org/record/6434459#.YILeV NPP30u>). The script used to generate values for the model parameters for the simulation is available in the Supplementary Information.

## Declarations

**Conflict of interest** The authors declare no competing interests.

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