# Opportunity costs resulting from scramble competition within the choosy sex severely impair mate choosiness

François-Xavier Dechaume-Moncharmont[*], Thomas Brom, Frank Cézilly

Université de Bourgogne-Franche-Comté, UMR CNRS 6282 Biogéosciences, Equipe écologie évolutive, Dijon, France

Studies on mate choice mainly focus on the evolution of signals that would maximize the probability of finding a good-quality partner. Most models of sexual selection rely on the implicit assumption that individuals can freely compare and spot the best mates in a heterogeneous population. Comparatively few studies have investigated the consequences of the mate-sampling process. Several sampling strategies have been studied from theoretical or experimental perspectives. They belong to two families of decision rules: best-of-$n$ strategies (individuals sample $n$ partners before choosing the best one within this pool) or threshold strategies (individuals sequentially sample the available partners and choose the first one whose quality exceeds a threshold criterion). Almost all models studying these strategies neglect the effect of scramble competition. If each paired individual is removed from the population of available partners, the distribution of partner quality dynamically changes as a function of the strategies of the other competitors. By means of simple simulations assuming opportunity costs, to the exclusion of all other costs, we show that scramble competition is a sufficient constraint to severely impair the evolution of choosy decision rules. In most cases, the evolutionarily stable strategy is to have a very low acceptance threshold or to sample two individuals at most in the population. This result may explain some discrepancies between predictions from previous models and their experimental validations. It also emphasizes the importance of considering the pairing process in studies of sexual selection.

© 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Mate choice is generally considered to be advantageous through fitness benefits accruing from mating with a high-quality individual (Andersson, 1994; but see Kokko, Booksmythe, & Jennions, 2014; Kuijper, Pen, & Weissing, 2012). Because females are most often the limiting sex, a majority of theoretical and empirical studies have focused on female choice, with female choosiness being defined as the effort a female is prepared to invest in mate assessment in terms of the numbers of potential males sampled or time spent per male (Castellano & Cermelli, 2011; Jennions & Petrie, 1997; but see also Reinhold & Schielzeth, 2014). Most models of female choice, however, rely on the implicit assumption that females are able to freely compare and easily spot the best partners in a large heterogeneous population. To what extent this assumption holds in natural populations is still a matter of debate (Castellano, 2009a; Lea & Ryan, 2015).

Various strategies of female choice can be considered from a theoretical point of view. In his seminal paper, Janetos (1980) contrasted two main decision rules: best-of-$n$ and fixed-threshold rules. The best-of-$n$ decision rule, which is sometimes also called pooled comparison (Uy, Patricelli, & Borgia, 2001; Wittenberger, 1983) or fixed-sample strategy (Wiegmann, Angeloni, Seubert, & Wade, 2013), is based on direct comparisons within a sample of males, and the subsequent choice of the one with the highest quality among them. The threshold decision rule, on the other hand, assumes that a female sequentially samples one male at a time, until she finds one whose quality exceeds an internal threshold criterion, which is sometimes called an internal standard (Leonard & Hedrick, 2009; Moore & Moore, 1988). The two decision rules differ strongly in their underlying cognitive assumptions. In the threshold decision rule the female is assumed to be able to calculate the value of the different options on an internal scale (Gibson, 1996; Moore & Moore, 1988). Conversely, the best-of-$n$ decision rule is based on direct scale-free comparisons which do not require the assessment of an absolute score for each individual encountered (Wiegmann, Real, Capone, & Ellner, 1996). However, the best-of-$n$ decision can also be a cognitively challenging task because the individual has to remember the identity, quality and

* Correspondence: F.-X. Dechaume-Moncharmont, Université de Bourgogne-Franche-Comté, UMR CNRS 6282 Biogéosciences, Equipe écologie évolutive, 6 boulevard Gabriel, 21000 Dijon, France.
E-mail address: fx.dechaume@u-bourgogne.fr (F.-X. Dechaume-Moncharmont).

location of several potential mates (Castellano, Cadeddu, & Cermelli, 2012; Leonard & Hedrick, 2009), and it relies on the assumption that the individual is able to transitively order the potential mates (Dechaume-Moncharmont, Freychet, Motreuil, & Cézilly, 2013; Lea & Ryan, 2015). Differences in cognitive abilities may then explain why the best-of-$n$ decision rule has mostly been reported in vertebrate species in which females are simultaneously assessing several males (Bensch & Hasselquist, 1992; Byers, Wiseman, Jones, & Roffe, 2005; Fiske & Kalas, 1995; Murphy & Gerhardt, 2002; Trail & Adams, 1989; Uy et al., 2001).

Two types of cost can, however, limit the efficiency of mate choice rules, direct costs and opportunity costs (Dombrovsky & Perrin, 1994; Janetos, 1980; Luttbeg, 1996; Real, 1990; Wiegmann et al. 1996; Wiegmann, Mukhopadhyay, & Real, 1999). First, direct searching costs, in terms of time, energy or predation risk, can strongly reduce the net benefit of mate choice (Jennions & Petrie, 1997, 2000; Hanna Kokko & Wong, 2007; Parker, 1983; Pomiankowski, 1987; Real, 1990; Wiegmann et al., 1996). Indeed, empirical observations suggest that females reduce their searching effort when the sampling costs are high (Bakker & Milinski, 1991; Bonachea & Ryan, 2011; Booksmythe, Detto, & Backwell, 2008; Byers et al., 2006; Godin & Briggs, 1996; Milinski & Bakker, 1992; Willis, Ryan, & Rosenthal, 2011). Models that take searching costs into account (Parker, 1983; Real, 1990) lead to two consistent predictions. (1) Females become less choosy when the searching costs increase. (2) Once searching costs are taken into account, threshold strategies dominate best-of-$n$ strategies (Real, 1990; Scheutz, Harris, & Boyd, 2010; Wiegmann, Seubert, & Wade, 2010), essentially because, by definition, a fixed-sample strategy such as the best-of-$n$ requires females to carry on sampling individuals even when they have encountered a high-quality male among the first sampled males. However, the best-of-$n$ rule is probably better at coping with a rapidly changing environment. If the distribution of male quality either locally or temporarily shifts towards higher values, a fixed-threshold strategy may result in mating with a partner of mediocre quality. The best-of-$n$ strategy, being scale free, automatically adjusts to rapid changes in the male quality distribution (McNamara & Fawcett, 2012).

Second, opportunity costs arise when a choosy female spends too much time on sampling a large number of mates before reaching a decision, such that, in the meantime, the chosen male has paired with another female (Etienne, Rousset, Godelle, & Courtiol, 2014; Pomiankowski, 1987; Real, 1990). Thus, the opportunity cost is strongly affected by the presence of competitors and empirical evidence suggests that individuals can become less choosy in the presence of same-sex competitors (Dale, Amundsen, Lifjeld, & Slagsvold, 1990; Lindström & Lehtonen, 2013). While the effect of competition within the chosen sex on mate choice has been widely investigated (review in Wong & Candolin, 2005), the effect of competition within the choosy sex has received less attention. It has, however, been suggested that the risk of remaining unmated should strongly reduce the female's acceptance threshold (Kokko & Mappes, 2005). This so-called 'wallflower effect' (De Jong & Sabelis, 1991; Kokko & Mappes, 2005) arises from difficulties females have finding available males due to low encounter rates, a female-biased sex ratio or reproductive asynchrony (review in Kokko & Mappes, 2005). Similarly, in the case of limited male encounter rates, females should tolerate a large inbreeding depression from mating with kin instead of waiting for possibly less-related mates that still have to be found (Kokko & Ots, 2006). However, for the sake of simplicity, these models assume a constant distribution of male quality.

The link between scramble competition and choosiness itself deserves closer attention. Searching strategies are influenced by competition within a population and in turn influence the intensity of competition. However, searching costs have generally been modelled as being simply proportional to the sampling effort. For instance, Real (1990) and Wiegmann et al. (1999) modelled the net expected fitness with a best-of-$n$ strategy as the expected fitness gain from mating with the best male in the sample set of $n$ males minus a cost term proportional to $n$ with a constant coefficient $c$, corresponding to the cost of sampling one individual (this marginal cost is measured in the same unit as the fitness gain due to the quality of the male). A female that has sampled 10 males is assumed to pay twice the cost paid by a female that sampled five males. On the one hand, this simple way of modelling the searching costs allows for the analytical expression of the optimal strategies. On the other, these models rely on the implicit assumption that the distribution of male quality does not vary across time (Wiegmann & Angeloni, 2007; Wiegmann et al., 1996). However, the sampling strategies of other individuals in the population are likely to dynamically modify the quality of the remaining partners if, once mated, the individual is not available for a long period of time (or during a time-out period). The probability of finding a good partner is therefore neither static nor an intrinsic property of a given strategy. It varies constantly over time and is a function of the frequency of the other strategies in the population.

The decision to sample one more male before reaching a decision is obviously more costly when the female faces intense competition than when she is alone in an infinite population of available partners. Several models (Collins & McNamara, 1993; Etienne et al., 2014; Ramsey, 2008) have investigated the effect of scramble competition on the threshold criterion. In an infinite population with a ratio $\alpha$ of number of females to number of males, the evolutionarily stable strategy (ESS) is to rely on the threshold criterion defined as the quantile above which lies the proportion $\alpha$ of best males (Collins & McNamara, 1993). For example, in a population in which there are two males for one female, the ESS strategy would be to accept any male whose quality is above the median male quality at the population level. In other words, as long as there are more males than females, the ESS threshold criterion guarantees that every female will find a male and that every male whose quality is above this quantile will be paired. This result has been generalized in finite-sized populations by Ramsey (2008). Here, we propose to extend these analyses of the ESS threshold in three directions. First, there is much experimental evidence that female choosiness decreases dramatically at the end of the courtship period or in the event of imminent spawning (Breedveld & Fitze, 2015; Kodric-Brown & Nicoletto, 2001; Lea, Halliday, & Dyson, 2000; Lynch, Stanely Rand, Ryan, & Wilczynski, 2005; Moore & Moore, 2001). We thus consider the last-chance option (Janetos, 1980): the female finally accepts the last encountered male irrespective of his quality. She is always certain to secure reproduction (as long as the sex ratio is female biased). This last-chance option is thus expected to favour choosy behaviour and lead the evolution of the ESS threshold towards larger values than in the absence of the last-chance option. Second, mate-sampling strategies have been reported to be sensitive to the uncertainty related to the assessment of female fitness gain from mating with a particular male (Castellano & Cermelli, 2011; Castellano, 2009b; Collins, McNamara, & Ramsey, 2006; Luttbeg, 1996, 2004; Phelps, Rand, & Ryan, 2006; Roff, 2015; Wiegmann & Angeloni, 2007). This uncertainty arises from limited sensory and cognitive abilities or because the information inferred from the observed male traits is noisy or conflicting (Castellano et al., 2012). We investigated how an imperfect assessment of male quality and the probabilistic decision could affect the female threshold criterion in a situation of scramble competition. Third, no model has investigated how the best-of-$n$ strategy evolves under competition. The best-of-$n$ rule has been criticized because it assumes that a previously

encountered mate can always be remembered and revisited (Dombrovsky & Perrin, 1994). Here, we investigated the effect of scramble competition which involves a continuous removal of partners: a previously unpaired partner might no longer be available when the female comes back to him later after having completed her sample set. However, this decision rule should be particularly robust in situations of strong competition. Even if all the previously sampled males have been chosen by other females in the meantime, the last one, at least, is still available.

## THE MODEL

Our goal was to assess the ESS in a self-consistent game-theoretic model (Houston & McNamara, 2002; Kokko & Wong, 2007; McNamara, 2013). While most previous studies have assumed a constant distribution of partner quality, we modelled the effect of scramble competition not as a constant cost, but as an emerging property of the other females' strategies. We assumed a simple situation in which females search for sedentary males. The intensity of competition arises directly from the sex ratio. We considered a stable population ($N_f$ females and $N_m$ males) within a species with seasonal reproduction and one reproductive event per season, which corresponds to a reproductive time-out longer than the courtship period for both sexes, as in the case of biparental care for instance. A female sequentially visits several males before choosing a partner and coming back to his nest to mate. The quality $w_i$ of male $i$ is defined on a one-dimensional continuous scale and is normally distributed (parameters: mean $\mu$ and standard deviation $\sigma$). Following Janetos (1980), we first used $\mu = 10$ and $\sigma = 1$ as default values, but we later assessed the sensitivity of the model's predictions to these parameters. With these default values, drawing a negative quality was highly improbable (99.9% of males have a quality between 6.7 and 13.3). However, the distribution was truncated at 0 in order to ensure that no male has a negative quality. Females have a directional preference for the highest quality males. For simplicity and tractability, they do not differ in fecundity, cognitive skills, sensory ability to locate an available mate and capacity to defend a territory once mated. Their fitness payoff is directly proportional to the quality of the chosen male, which they are capable of estimating from male indicator characters (Wiegmann et al., 2013).

At the beginning of each generation, all individuals are unpaired. We modelled asynchronous encounters between females and available males as a Poisson process (Mangel & Clark, 1988). For a given female, the time until the next encounter was a random variable following an exponential distribution (constant rate parameter $r = 1$). Therefore, females sample males in random order, and some females start searching earlier than others. Two females cannot sample the same available male at the same time. When it is the turn of a given female to sample a male, one male is randomly sampled from the pool of available males (provided that there is still at least one unmated male in the population). As soon as a female accepts a male, they form a stable pair and they are both removed from the pool of single individuals. The distribution of quality of the available mates thus changes continuously as a direct consequence of scramble competition between females. Individuals only mate once in each breeding season. We assume no extrapair copulation, and paired individuals have no further opportunity to reproduce. A female's fitness is proportional to the quality $w_i$ of her partner $i$. Our aim was to investigate the effect of opportunity costs, disregarding any other potential confounding factors that are already expected to decrease choosiness. We therefore assumed a constant encounter rate independent of the number of available males and no direct sampling cost (such as travel cost, energy expenditure or risk of predation). There was no effect of reproduction timing either (Dunn, Winkler, Whittingham, Hannon, & Robertson, 2011; Kokko, 1999): two females that pair with males of identical quality, but at different times in the season, have the same resulting fitness. The only benefit of pairing early is to secure a partner: choosy females might never find a male because less choosy females generally make a quicker decision.

### Decision Rules

We considered two decision rules: threshold and best-of-$n$ (Janetos, 1980). Under the threshold decision rule, a female rejected every male until she met one with a quality $w_i$ higher than her critical threshold value $w_c$. We let the females sample the available males until the number of pairs converged to a steady state. Some females remained unpaired because their threshold criterion was too high and there were no males reaching the minimal quality. When the last-chance option (Janetos, 1980) was considered, these females were then paired with the next sampled male. Recalls were possible: a female using a threshold decision rule could randomly sample a previously sampled male again (Wiegmann et al., 1996).

The best-of-$n$ decision rule assumes that the female samples $n$ males before choosing the best one within this pool. In our simulation, a female sequentially sampled the available males, assessed their qualities and memorized their locations until she had completed her pool of $n$ different partners. She finally ranked these males according to their quality, and came back to the nest of the best male. If the male was still available, they immediately paired. It was also possible that, meanwhile, this best male had already been chosen by another female and was no longer available. So the female came back to the next best male, and so on. All the previously visited males could be paired, except the very last one. A female only visited males that were available at the time step of the sampling. By definition, her last male was thus always single when she finally compared the potential partners and made her decision. Consequently, as soon as she had completed her pool of $n$ males, she was certain to secure at least one mate (but not necessarily the best of the sample set). The worst case scenario for a choosy female would be to not find enough available males while trying to complete a large collection of $n$ males. In that case, she chose from among the available ones, if any, in her incomplete sample set.

### Calculation of the ESS

The calculation of the ESS was performed separately for each decision rule; we did not confront one decision rule against the other in the same population. When exploring the threshold decision rule, the strategy of a given female was defined by her threshold criterion $w_c$. For the best-of-$n$ decision rule, the strategy of a given female was defined by the number $n$ of males sampled before choosing the best one. The value of $n$ was not necessarily a discrete number. We allowed continuous values of $n$ assuming stochastic behaviour: for example, a female following the mixed-strategy best-of-3.2 had a probability of 0.8 of sampling three males, and a probability of 0.2 of sampling four males (McNamara, Webb, Collins, Székely, & Houston, 1997). A large value of $w_c$ or $n$ indicated a high level of choosiness which would theoretically allow a female to find a high-quality male if she was alone in a large population of males. However, the fitness of a female following a given strategy was strongly dependent on the frequency of the other strategies in the population through the background distribution of an available male's quality.

For each set of parameters, we used genetic algorithms to calculate the ESS value (Fawcett & Bleay, 2009; Kuijper et al., 2012). We evolved the mate search strategies by iterating a simplified process of mutation and selection over a large number of successive

breeding seasons. The population size $(N_m + N_f)$ and sex ratio $s = N_m/(N_m + N_f)$ were kept constant. We assumed that after each breeding season, a new generation replaced the previous one. The strategy of the $N_f$ new females was inherited from the strategy of the previous females. The frequency of a given strategy in the population was a function of its relative outcome in the previous generation. The probability $p_j$ that a female inherited her strategy from female $j$ from the previous generation was

$$p_j = \frac{w_j}{\sum_{i=1}^{N_f} w_i}$$

where $w_j$ was the fitness of the female $j$ (i.e. the quality of the male she mated). If female $j$ did not succeed in finding a male ($w_j = 0$), her strategy was not transmitted to the next generation. Accepting a low-quality male ($w_i > 0$) was still better than no reproduction at all, because if a female remained unmated, she ended up with null fitness. We started from a homogeneous population with a resident strategy in which all females adopted an arbitrarily chosen value of $n$ (for the best-of-$n$ decision rule) or critical value $w_c$ (for the threshold decision rule). With a probability of 0.05 for each generation, one randomly sampled female inherited the strategy from her mother but with a small normally distributed mutation, with a mean centred on 0 and a variable standard deviation. This standard deviation was adjusted during the simulation to improve ESS search. The large initial value (SD = 0.5) allowed extensive exploration of the possible strategies and quick convergence of the algorithm. As the mean strategy value reached an equilibrium, we decreased the standard deviation of the mutation (SD = 0.02) in order to limit the effect of the stochastic noise on the estimation of the ESS and the corresponding fitness gain (Poethke & Hovestadt, 2002).

If the mutation increased the female's fitness, her strategy could therefore spread in the population and become the new resident. In contrast, a mutant strategy that was less efficient than the resident strategy disappeared. The process was iterated (typically over 1500 generations) until no mutant outperformed the resident population and the simulation reached a steady state (less than 0.1% of variation for the value of the estimated ESS). We verified that the arbitrarily chosen initial condition had no effect on the final steady state (Fig. 1). To assess the strength of the evolutionary response (Hereford, Hansen, & Houle, 2004), we also estimated the shape of the fitness landscape in the neighbourhood of the ESS. We calculated the difference between the average fitness of the resident strategy at the ESS ($\overline{w^*}$) and the fitness of one single mutant ($w_m$) standardized by $\sigma_w$ the fitness standard deviation in the population: $\Delta w = (w_m - \overline{w^*})/\sigma_w$. This gives the fitness cost of the mutation in units of fitness standard deviation.

### Sensitivity Analysis

The model had a limited number of variables in order to keep it tractable. The main variable was the sex ratio $s$, which can be strongly male biased in natural populations (Donald, 2007; Kosztolányi, Barta, Küpper, & Székely, 2011). Values of $s$ lower than 0.5 corresponded to an excess of females and intense scramble competition, while a value of $s$ larger than 0.5 corresponded to an excess of males and more opportunities for mate choice. The number of females was kept constant ($N_f = 100$) as preliminary simulations showed that larger population sizes had only a marginal effect on the estimated values of the ESS while they considerably increased the calculation time. A smaller $N_f$ value quantitatively (but not qualitatively) modified the predictions. We also assessed the effect of the distribution parameters (mean and
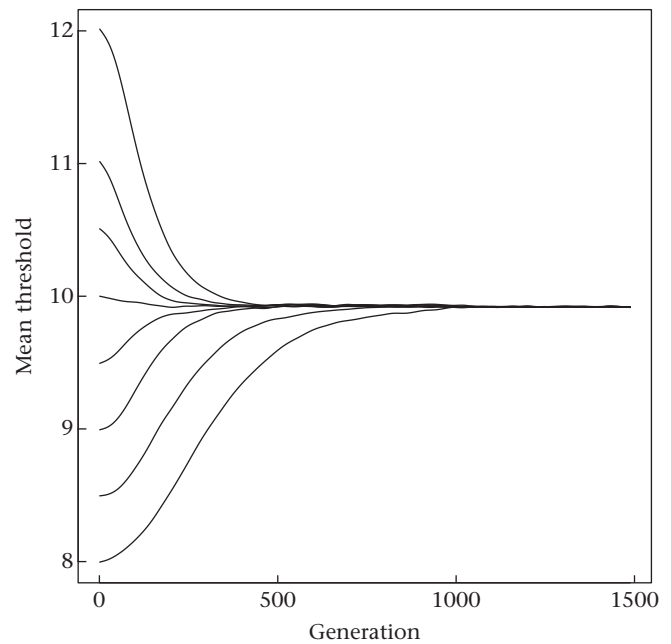


**Figure 1.** Example of ESS calculation using a genetic algorithm for the threshold decision rule with the last-chance option. Each curve corresponds to an initial strategy. We started with homogeneous populations of 100 females and 150 males (sex ratio $s = 60\%$ males; the male quality followed a normal distribution with parameters $\mu = 10$ and $\sigma = 1$). A female contributed to the next generation proportionally to her fitness (i.e. the quality of her mate). Daughters inherited the threshold criterion of their mother with rare random mutation. If a mutation improved the fitness of the female, its frequency increased in the population and modified the mean strategy at the population level. For each initial value of the threshold criterion, the ESS was calculated as the mean strategy of 10 000 populations at equilibrium after 1500 generations.

variance) for male quality on the predicted ESS values (Wiegmann et al., 2013).

### Error-prone Response

In the threshold decision rule model described above, a female based her pairing decision on a perfect assessment of the encountered male's quality. The threshold is a step function with a clear separation between males that were always rejected and those that were always accepted. This clear-cut discrimination between males is unlikely in nature (Valone, Nordell, Giraldeau, & Templeton, 1996), especially when male quality is only weakly correlated with female preference (McLean, Bishop, & Nakagawa, 2012). We thus considered the decision process to be subject to errors (Fawcett & Johnstone, 2003; Houston, 1997; Johnstone, 1997; McNamara et al., 1997). A female had a probability $q$ of accepting a male which depended on the difference between the male's quality $w_i$ and the female's threshold criterion $w_c$:

$$q = \frac{1}{1 + \exp[-\lambda(w_i - w_c)]}$$

This probability tended towards 1 when the difference ($w_i - w_c$) increased towards large positive values, and towards 0 in the opposite situation. The probability of an error decreased as its cost increased: when a male had a much higher (much lower) quality than the female's threshold, she accepted him with a high (low) probability. When the male's quality was close to the female's threshold criterion, the female's decision was subject to frequent errors. Parameter $\lambda$ controlled the weight given to the errors on mate choice. Large values of $\lambda$ corresponded to a precise assessment

of male quality compared to the threshold and a sharp transition between males that were always rejected and those that were always accepted. As $\lambda$ decreased, there was an increasing probability of accepting a male whose quality was lower than the threshold, or rejecting a male whose quality was higher than the threshold criterion.

All the simulations were performed using the R programming language (R Core Team, 2015).

## RESULTS

The sex ratio had a similar effect on the ESS for both the threshold (Fig. 2a) and best-of-$n$ (Fig. 2b) decision rules. When there were fewer males than females, neither of the strategies could outperform random choice. For the best-of-$n$ decision rule, the ESS was best-of-1, i.e. to always accept the first encountered male, which is identical to random choice strategy (Fig. 2b). The calculation of the ESS for the threshold decision rule led to analogous conclusions. The strategies converged to low threshold criteria ($w_c \approx 7.5$, Fig. 2a), which corresponds to random choices. In the case of pure random choice, the threshold is expected to be equal to or lower than the minimal male's quality. The genetic algorithm should theoretically converge towards infinitely low thresholds: a finite, albeit very low, threshold leads to rare rejections of bad quality males. Such a suboptimal strategy should be counterselected by the algorithm. However, because very low-quality

males were exceptional in a finite population, the genetic algorithm converged towards finite thresholds which were sufficient to accept almost every male. Simple Monte Carlo simulations show that if one draws a set of 100 independent random numbers that are normally distributed ($\mu = 10$, $\sigma = 1$), the expected minimum value would be approximately 7.5. For both decision rules, females engage in a 'generalized war of attrition' (Mohamad et al., 2015), and they are forced to be less choosy than their competitors: the first female trying to increase her choosiness exposes herself to the risk of remaining unmated.

At even sex ratios, the abrupt increase in choosiness with the best-of-$n$ decision rule (Fig. 2b) was due to the fact that every female was certain to mate with a male, even if he happened to be a low-quality one. Females only assessed the quality of a single male at the time of the sample. Thus, the last male visited, at least, was available. This was also true for the threshold decision rule with the last-chance option (Fig. 2a, thick line), which led unsuccessful females to finally accept one of the remaining low-quality males. Females were certain to mate under a male-biased sex ratio. In contrast, without a last-chance option, a choosy female was not certain to find a male: the ESS for the threshold decision rule without the last-chance option slowly increased without a sharp transition around an even sex ratio (Fig. 2a, dashed line), and remained lower than the ESS for the threshold strategy with a last-chance option. For sex ratios larger than 0.5, the curve of the ESS threshold without the last-chance option perfectly matched the values predicted by Collins and McNamara (1993). When the sex ratio became strongly male biased, ESS choosiness increased but in order to observe a threshold criterion higher than the average male quality (which would not be considered as a very high level of choosiness in many sexual selection studies), there must be at least twice as many males as females ($s > 0.66$). When the resident population was at the ESS, a mutant increasing her threshold value by one standard deviation of male quality ($\sigma$) suffered from a $0.26\,\sigma$ decrease in her expected fitness payoff for $s = 0.5$ (Fig. 3a) and a $0.37\,\sigma$ decrease for $s = 0.6$ (Fig. 3b). The best-of-$n$ decision rule followed the same qualitative properties, with a sharp transition around an even sex ratio. The choosiness then increased with the number of available males per female (Fig. 2b). When there were twice as many males as females, the ESS was to compare four males (best-of-4). By comparison, with the threshold decision rule without a last-chance option at the same sex ratio, females that found a male meeting the criteria of their ESS value sampled 3.6 males on average. When the resident population was at the ESS, a mutant increasing her sample size by two males suffered a decrease in her fitness payoff of $0.80\,\sigma$ for $s = 0.5$ (Fig. 3c) and $0.10\,\sigma$ for $s = 0.6$ (Fig. 3d).

The two decision rules (at their corresponding ESS value) led to a very close expected fitness gain (Fig. 4) around an even sex ratio. With a female-biased sex ratio, the ESS was to mate randomly and the expected fitness gain $E(w)$ thus decreased as a function of the sex ratio $s$, and the mean male quality $\mu$: $E(w) = \mu s/(1 - s)$. With an increasingly male-biased sex ratio, both decision rules led to a regularly increasing fitness gain while the best-of-$n$ decision rule exhibited a slightly lower gain than the threshold decision rule. For large proportions of males, the threshold strategy dominated the best-of-$n$ strategy. This was expected because the best-of-$n$ strategy does not target any given male quality. If a female following a best-of-3 strategy samples three low-quality males, she will accept one of them. In addition, the best-of-$n$ strategy is somewhat more rigid than the threshold strategy. It forces the female to complete her sample of $n$ males, even when she has already found a high-quality male earlier during the sampling process. In addition, at the end of the process, a female could be forced to accept a very low-quality male from those remaining in her sample set. This is
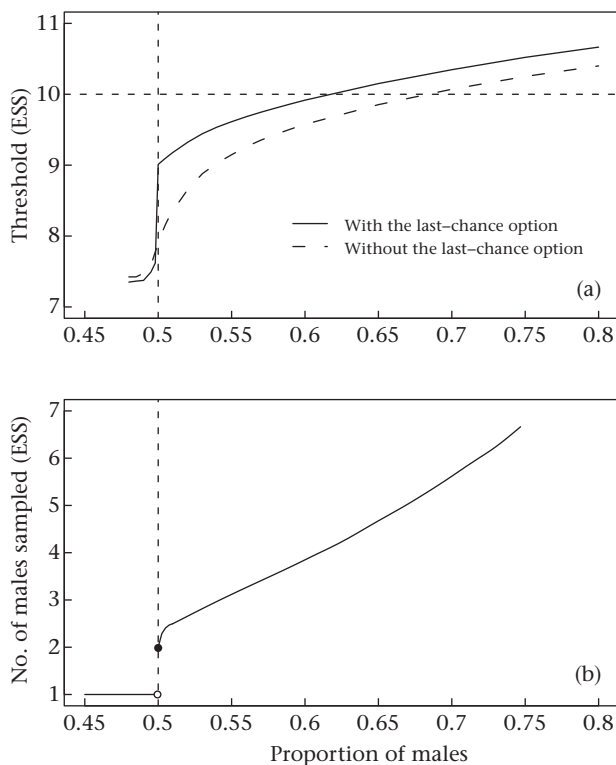


**Figure 2.** Evolutionarily stable strategies as a function of the sex ratio (proportion of males). For a given sex ratio value, the ESS was estimated using the genetic algorithm as the mean strategy over 10 000 populations at equilibrium (Fig. 1). The male quality followed a normal distribution ($\mu = 10$ and $\sigma = 1$). (a) Threshold decision rule with (continuous line) or without (dashed lines) the last-chance option. The horizontal dashed line shows the mean quality of the males. Because low-quality males were rare, the genetic algorithm was unable to accurately converge towards extremely low values for the threshold criterion, and any threshold criterion $w_c < 7.5$ corresponded to a random choice strategy. (b) Best-of-$n$ decision rule. The ESS is defined by the mean number of males sampled before choosing a mate. The ESS function is right continuous: for a perfectly even sex ratio (vertical dashed line), the ESS is best-of-2.
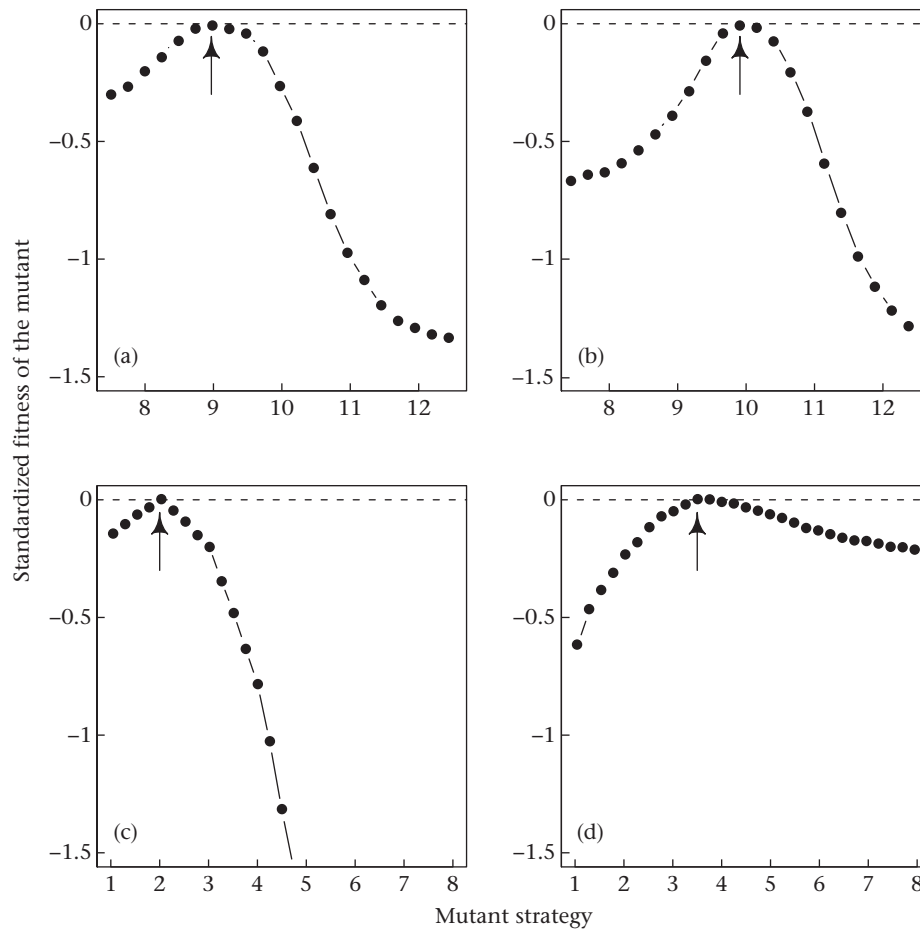
**Figure 3.** Assessment of the strength of the evolutionary response around the ESS for the two decision rules and two values of the sex ratio. Assuming a single mutant in a resident population at the ESS (as defined in Fig. 2), the cost of the deviation from the ESS was estimated as the standardized fitness of the mutant: the difference between its absolute fitness of the mutant $w_m$ and the average fitness of the resident strategy $\overline{w^*}$ divided by the fitness standard deviation $\sigma_w$. This gives the fitness cost of the mutation in units of fitness standard deviation. Except when the mutant strategy is the same as the ESS (indicated by the arrow), the standardized fitness of the mutant is negative. The male quality followed a normal distribution ($\mu = 10$ and $\sigma = 1$). (a) Threshold decision rule, proportion of males $s = 0.5$. (b) Threshold decision rule, $s = 0.6$. (c) Best-of-$n$ decision rule, $s = 0.5$. (d) Best-of-$n$ decision rule, $s = 0.6$.

not usually the case with the threshold decision rule. The ESS threshold criterion guarantees that every female finds a male within the top ranked males.

When the male quality variance increased while the mean was kept constant (Fig. 5a), the ESS for the best-of-$n$ rule remained constant. This was expected because it is a comparative rule based on rank and not the absolute value of the potential mate (McNamara & Fawcett, 2012). For the threshold decision rule with a last-chance option, the absolute value of the ESS either decreased or increased with the variance as a function of the sex ratio (Fig. 5b). This behaviour is consistent with that predicted by Collins and McNamara (1993) for the threshold decision rule without a last-chance option. In their model, the ESS threshold criterion was the upper quantile of the male quality distribution which corresponded to a proportion of males equal to the ratio of the number of males over the number of females. In a large population, the ESS threshold corresponded to the maximal male quality which guarantees that when $f$ females are paired, the $f$ best males have been chosen. When there were at least two males per female, the ESS threshold was larger than the median quality of the males and the absolute value of the threshold should increase when the male quality variance increases. With lower proportions of males, the ESS threshold lies below the median male quality and therefore should decrease

when the variance increases. We observed the same pattern with the last-chance option. The absolute value for the ESS threshold criterion corresponded to a quantile of the male quality distribution. Once this value was standardized $w_c' = (w_c - \mu)/\sigma$, the threshold criterion $w_c'$ corresponded to a distance to the mean quality and was measured in standard deviation units. This standardized ESS threshold criterion $w_c'^*$ remained constant when the variance of the male quality distribution changed (Fig. 5c). Irrespective of the variance or the mean quality distribution, as long as the worst males had a low probability of leading to null fitness (no large overlap of the quality distribution with zero), the ESS criterion can therefore be seen as a constant percentile of the male population. The female should accept or reject a male as a function of his rank in the population and not as a function of the absolute value of his quality. The mean male quality had only limited effect on the ESS (see Appendix).

The precision of the male's quality assessment for a female using a threshold decision rule had an effect on choosiness (Fig. 6). Increasing the uncertainty (a higher probability of accepting a low-quality male or rejecting a high-quality male) led to decisions being made more cautiously and a higher level of choosiness. However, too much uncertainty made the process of quality assessment difficult and the ESS choosiness decreased.
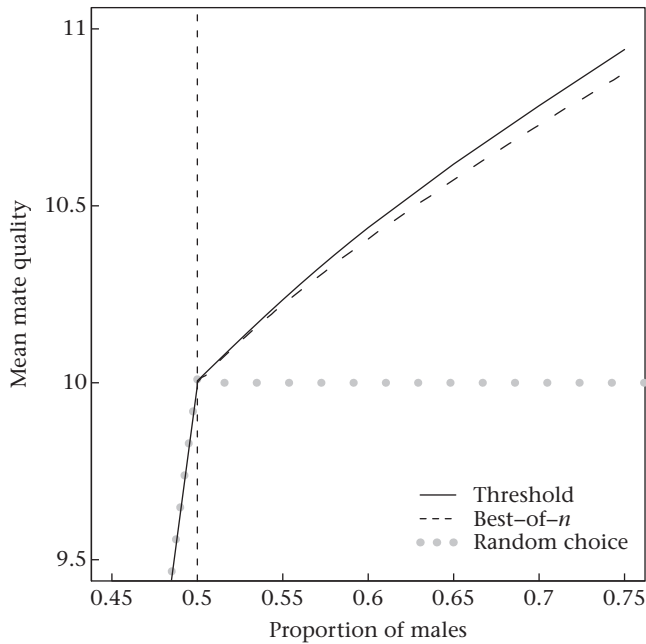
**Figure 4.** Mean fitness gain as a function of the sex ratio for the threshold decision rule with the last-chance option (continuous line) and the best-of-*n* rule (dashed line). The fitness gain of each rule was estimated as the mean quality of the males chosen by the females using the ESS criterion predicted for the corresponding sex ratio (as illustrated in Fig. 2). The quality of the males was normally distributed ($\mu = 10$ and $\sigma = 1$). The vertical dashed line shows an even sex ratio. The horizontal dotted line shows the expected fitness with random choice. With female-biased sex ratios, the mean fitness gain with random choice decreased with the sex ratio as not all of the females managed to find a male.



**Figure 5.** Comparison of ESS choosiness as a function of the variance of male quality. (a) Probability density function of the males' quality for three normally distributed populations centred around the mean value $\mu = 10$ and with a standard deviation of either $\sigma = 1$, $\sigma = 2$ or $\sigma = 4$. (b) ESS for the threshold criterion with the last-chance option as a function of $\mu$ and the proportion of males: $s = 0.5$ (triangle), 0.6 (cross) and 0.75 (black circle). (c) Standardized value for the ESS threshold criterion. The parameters and key are the same as in (b).

## DISCUSSION

Opportunity costs arising from scramble competition represent a sufficiently strong constraint to severely reduce and, in many cases, almost suppress female choosiness. Importantly, this result holds even when there are more available males (chosen sex) than females (choosy limited sex). More generally, non-negligible opportunity costs are a crucial component of decision making under scramble competition, and they should be observed in all contests for possession, consumption or use of any indivisible goods (whether they are sexual partners, nest sites or territories). For simplicity and tractability, we did not consider any sampling costs other than opportunity costs. It was a conservative assumption because the addition of other sampling costs, such as energy cost, risk of predation, risk of injuries during competition for a mate or time cost, has been reported to decrease choosiness in many models (Fawcett & Johnstone, 2003; Pomiankowski, 1987; Real, 1990; Wiegmann et al., 1996).

In many species, choosiness has been reported to increase when the number of competitors decreases (Kvarnemo & Simmons, 1999; Lindström & Lehtonen, 2013; Madden & Whiteside, 2013; Schacht & Borgerhoff Mulder, 2015; Stoffer & Uetz, 2015), eventually leading to a sex role reversal in the case of a biased operational sex ratio. The more abundant available sex is assumed to be more intrasexually competitive than the limited sex because there is a lack of available partners at any one time (Berger-Tal & Lubin, 2011; Kvarnemo & Ahnesjö, 1996). However, this does not mean that there is no competition at all among the limited sex. As pointed out in the review by Rosvall (2011), females rarely compete for a number of mates; they mainly compete for high-quality partners. Care should thus be taken to avoid thinking that female intrasexual competition rarely evolves within a strongly male-biased population.
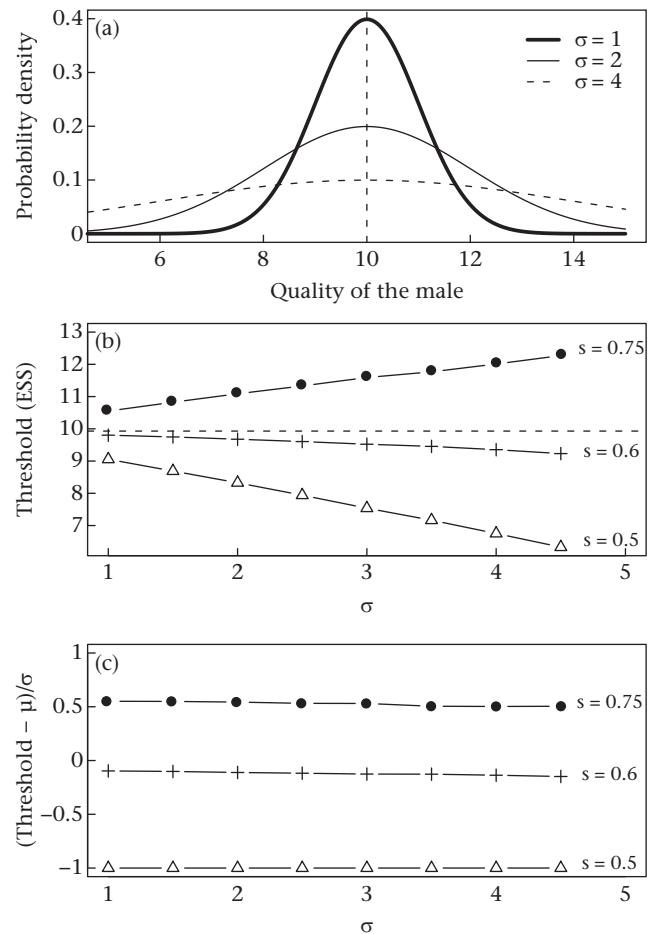
The benefit of choosing a good partner is not always as large as it may appear at first sight. Random mate choice could be an adaptive strategy in many situations. For instance, it is useless (or even costly) to be choosy if only the best males manage to control a territory (Meuche, Brusa, Linsenmair, Keller, & Prohl, 2013) or exhibit sexual displays over a lengthy period of time (Castellano, 2009b; Friedl & Klump, 2005). In such situations, the probability of large fitness gain is sufficiently high when randomly picking a male or when simply mating with the closest one. Even extreme costs, such as a high risk of being cannibalized (Barry & Kokko, 2010) or a large inbreeding depression (Kokko & Ots, 2006) arising from mating with a carelessly chosen partner, do not systematically lead to a high level of choosiness when the mate encounter rate is low. Therefore, observations of mating patterns consistent with random mating have been reported in several field studies (review by Castellano et al., 2012).

### Experimental Assessment of the Decision Rules

Several authors have discussed whether one can infer the female's decision rule by experimentally manipulating male quality
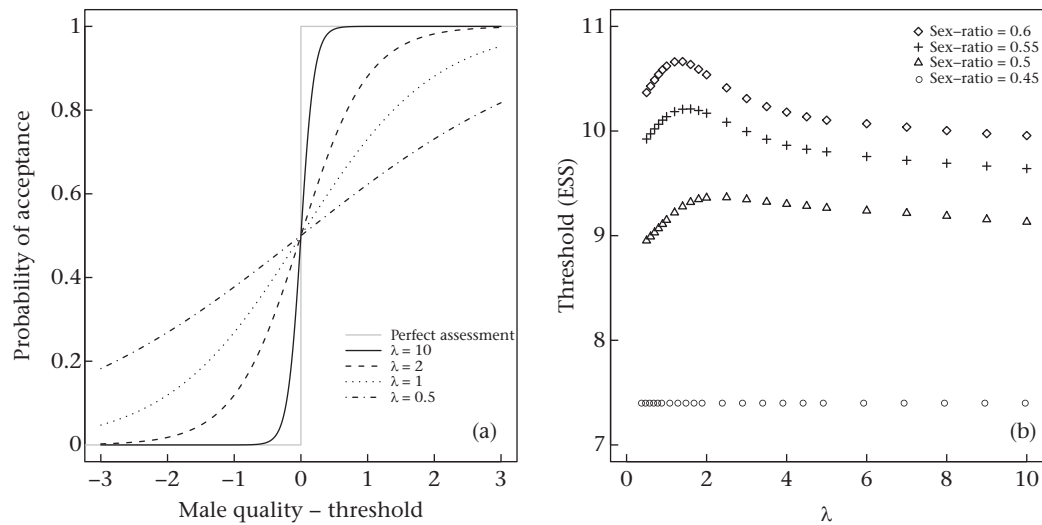
**Figure 6.** Consequences of an imperfect assessment of the male quality on the threshold decision rule with the last-chance option. (a) The probability of accepting a male as a function of the difference between his quality and the female threshold criterion. When a female is capable of a nearly perfect assessment (large $\lambda$ value, see text), she only accepts a male if his quality is higher than her threshold criterion. For smaller $\lambda$ values, the probability is a less steep function leading to a higher probability of error (accepting a low-quality male or rejecting a high-quality male). (b) Effect of $\lambda$ on the ESS for several proportions of males. The quality of the males was normally distributed ($\mu = 10$ and $\sigma = 1$).

distribution (Roff, 2015; Seubert, Wade, & Wiegmann, 2011; Wiegmann et al., 2013, 1996). It is an important and complex question. So far, experimental studies have not allowed researchers to unambiguously identify the sampling strategy followed by animals because sampling behaviours seem to be compatible with both decision rules (Castellano et al., 2012). If one could rely on strategy-specific predictions about female behaviour as a function of the male quality distribution, it would be very useful to design efficient experimental set-ups to investigate mate-sampling strategies.

With that in mind, Seubert et al. (2011) compared optimal thresholds in two populations with different distributions of male quality. When the male quality from these two populations was normally distributed with the same mean value, the distribution with lower variance was stochastically dominant over the other at the second order. In this situation, the authors predicted that the optimal threshold value should always be higher for a female in the population with the highest male variance. However, this analytical result only holds if one assumes constant (eventually null) searching costs and a constant quality distribution. With scramble competition, these two assumptions no longer hold. Scramble competition constantly modifies the distribution of available mates and induces variable opportunity costs. When one takes opportunity costs into account not as a constant but as a dynamic constraint emerging from the sampling process itself, the absolute value of the ESS threshold appears to be strongly dependent on the sex ratio. Our simulation partly confirmed some of Seubert et al.'s (2011) results: in a situation of very low competition (more than two males for one female), the ESS threshold increased with the variance. However, we also found the opposite result in more competitive situations (fewer than two males for one female): the absolute ESS threshold decreased with the male variance. This example illustrates the crucial importance of taking the effects of the perceived competition into account in mate-sampling experiments. For instance, rearing conditions involving a high density of same-sex individuals could induce a strong bias in the perception of competition by the females and thus severely decrease their choosiness at a later time during mate choice experiments.

Our results could also partly explain the apparently suboptimal behaviours reported in 'secretary problem' experiments, a classic optimal stopping problem in economics (Ferguson, 1989; McCall & McCall, 2008), which can immediately be interpreted as a mate choice problem. The problem is stated as follows. A recruiter has to choose one (and only one) secretary from among a finite set of *n* candidates. He interviews them sequentially. During the interview, he can immediately and precisely estimate their quality. He then has to decide whether he accepts the candidate (and rejects all the remaining candidates without interviewing them), or he rejects the candidate and never sees her again. Human subjects in these experiments have been observed to terminate their search much sooner than the predicted optimal strategy (Seale & Rapoport, 1997, 2000). Several alternative decision rules (for instance, rules based on ranks or a predetermined number of high-quality candidates) have been proposed in order to reduce the discrepancies between theoretical predictions and experimental observations (Bearden & Murphy, 2007; Stein, Seale, & Rapoport, 2003). However, the calculation of optimal strategies in the 'secretary problem' assumes no effect of scramble competition (but see Collins & McNamara, 1993; Ramsey, 2008). If one considers that most sampling strategies have evolved to cope with highly competitive situations, it is possible that subjects adopt a low level of choosiness because it is a generally adaptive strategy under scramble competition. What appears to be a cognitive bias could be adaptive in a more realistic ecological context (Fawcett et al., 2014; Kacelnik, 2006; Todd & Gigerenzer, 2012).

*Decision Rule under Uncertainty*

Our simulations predicted a nonmonotonic effect of uncertainty in the assessment of male quality. The ESS level of choosiness first increased when the reliability of the cues regarding male quality decreased. We then observed a decrease in choosiness when the assessment reliability decreased too much: if there is not enough information to be gained from assessing a given quality cue, it is useless to be choosy with respect to that cue. This result is not fully consistent with the analytical predictions by Wiegmann and Angeloni (2007) in a nongame-theoretical model. These authors

assumed that the expected fitness gain from pairing with a given male was a random variable defined from both observed and unobserved male attributes. The level of uncertainty in the quality assessment, which increased the variance of the potential fitness gain for the female, did not affect the optimal threshold criterion. However, in their study, the mate quality distribution was assumed to remain constant and was not a function of the other female strategies.

Our simulation might explain why some experimental studies have reported apparently contradictory results. In the wolf spider, *Schizocosa floridana*, females rely on both visual and seismic courtship signals to assess male quality. The use of these multimodal signals is reported to facilitate the detection of available partners and increase information about mate quality (Candolin, 2003). When they could not rely on visual cues and only used one component of the multimodal signal (which should reduce the accuracy of the mate quality assessment), the choosiness of the females increased (Rundus, Sullivan-Beckers, Wilgers, & Hebets, 2011). In contrast, female three-spined sticklebacks, *Gasterosteus aculeatus*, spent less time searching and visited fewer males in the absence of visual stimulation (Heuschele, Mannerla, Gienapp, & Candolin, 2009). It is possible that the level of uncertainty was lower in the first experiment than in the second, leading to an increase in choosiness in the former and a decrease in the latter.

In our model, the assessment error was assumed to be independent of the threshold criterion: for instance, the probability of accepting a male whose quality was lower than the female threshold criterion by one unit of standard deviation was the same when the threshold corresponded to the mean of the male quality distribution or to the top 5% of males. It is possible that the assessment precision is higher for the best or worst males than for the medium quality ones. For the sake of simplicity, we also assumed a linear functional relationship between the perceived male quality and the female's fitness gain. However, it is possible that the perceived male quality is translated in terms of female fitness gain, assuming a nonlinear (for instance, concave) function (Wagner, 1998; Widemo & Saether, 1999; Wiegmann et al., 2013). The predicted level of the optimal threshold or number of males sampled could thus be quantitatively different (Wiegmann et al., 2013, 1999).

Individuals can also optimize their assessment effort (for instance, by spending more time assessing each candidate) as a function of the level of perceptual errors (Abbott & Sherratt, 2013; Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006; Chittka, Skorupski, & Raine, 2009; Trimmer et al., 2008). Following Wiegmann and Angeloni (2007) and Phelps et al. (2006), in order to keep our model simple, the level of uncertainty was a given property of the environment; females could not lower the risk of accepting a low-quality partner by increasing the effort put into cue assessment. In uncertain environments, one strategy of the female could be to increase the time spent evaluating each individual rather than increasing the total number of sampled partners. In a nongame-theoretical situation, Castellano and Cermelli (2011) showed that both the threshold level and the time spent evaluating prospective mates decreased as the time cost increased. When one adds the effect of scramble competition, ESS choosiness could be affected by the possibility of trading speed for precision.

*Alternative Mate-sampling Strategies*

The aim of this paper was to emphasize the importance of opportunity costs arising from scramble competition. We have therefore focused our attention on the two most extensively studied decision rules in mate choice instead of systematically investigating all the alternative rules proposed in the literature: a

decision based on prior information about the distribution of mate quality at the population level (Castellano et al., 2012; Dombrovsky & Perrin, 1994; Mazalov, Perrin, & Dombrovsky, 1996); a decision rule that is flexible across the season or towards the end of the reproductive or courtship period (Bleu, Bessa-Gomes, & Laloi, 2012; Dukas & Baxter, 2014; Johnstone, 1997; Ramsey, 2008); and a decision relative to female quality (Beckers & Wagner, 2011; Cotton, Small, & Pomiankowski, 2006) or competitive ability (Fawcett & Johnstone, 2003; Härdling & Kokko, 2005; Venner, Bernstein, Dray, & Bel-Venner, 2010). More generally, pair formation can result from mutual mate choices (Alpern & Katrantzi, 2009; Bergstrom & Real, 2000; Johnstone, 1997; Johnstone, Reynolds, & Deutsch, 1996; Ramsey, 2011; Real, 1991). We modelled a simplified situation in which territorial males were passively visited by mobile females. However, even territorial males can express choice through their motivation to engage in courtship or, in contrast, to chase a low-quality female away (Rowell & Servedio, 2009).

*Conclusion*

The variation in female mating decisions has been poorly investigated despite its central role as a selective force acting on the evolution of male traits (Cotton et al., 2006). However, the level of female choosiness is highly constrained by scramble competition. The effects of opportunity costs described herein are far from negligible. They should considerably decrease the strength of sexual selection. Sexual selection models have classically discussed the effect of preference on competition, but there is a complex interplay between the preference functions and patterns at the population level. In our model, the opportunity cost can be seen as an emerging property of competition resulting from the bias of the (operational) sex ratio, and in turn it shapes the ESS level of choosiness. Future models of coevolution between male traits and female preferences should take into account the dynamical effect of competition within the choosy sex. The opportunity costs should decrease female choosiness and, therefore, the intensity of sexual selection. One cannot simply dismiss this effect on the basis that there are generally many more males than females. Our study exemplifies that non-negligible opportunity costs can arise even in the case of a strongly male-biased operational sex ratio.

**References**

Abbott, K. R., & Sherratt, T. N. (2013). Optimal sampling and signal detection: unifying models of attention and speed–accuracy trade-offs. *Behavioral Ecology, 24*(3), 605–616. http://dx.doi.org/10.1093/beheco/art001.

Alpern, S., & Katrantzi, I. (2009). Equilibria of two-sided matching games with common preferences. *European Journal of Operational Research, 196*(3), 1214–1222. http://dx.doi.org/10.1016/j.ejor.2008.05.012.

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press. Retrieved from http://www.worldcat.org/isbn/0691000573.

Bakker, T. C. M., & Milinski, M. (1991). Sequential female choice and the previous male effect in sticklebacks. *Behavioral Ecology and Sociobiology, 29*(3), 205–210. http://dx.doi.org/10.1007/BF00166402.

Barry, K. L., & Kokko, H. (2010). Male mate choice: why sequential choice can make its evolution difficult. *Animal Behaviour, 80*(1), 163–169. http://dx.doi.org/10.1016/j.anbehav.2010.04.020.

Bearden, J. N., & Murphy, R. O. (2007). On generalized secretary problems. In M. Abdellaoui, R. D. Luce, M. J. Machina, & B. Munier (Eds.), *Uncertainty and risk: Mental, formal, experimental representations* (Vol. 41, pp. 187–205). Berlin, Germany: Springer. http://dx.doi.org/10.1007/978-3-540-48935-1_11.

Beckers, O. M., & Wagner, W. E. (2011). Mate sampling strategy in a field cricket: evidence for a fixed threshold strategy with last chance option. *Animal Behaviour, 81*(3), 519–527. http://dx.doi.org/10.1016/j.anbehav.2010.11.022.

Bensch, S., & Hasselquist, D. (1992). Evidence for active female choice in a polygynous warbler. *Animal Behaviour, 44*, 301–311. http://dx.doi.org/10.1016/0003-3472(92)90036-9.

Berger-Tal, R., & Lubin, Y. (2011). High male mate search costs and a female-biased sex ratio shape the male mating strategy in a desert spider. *Animal Behaviour, 82*(4), 853–859. http://dx.doi.org/10.1016/j.anbehav.2011.07.021.

Bergstrom, C. T., & Real, L. A. (2000). Towards a theory of mutual mate choice: lessons from two-sided matching. *Evolutionary Ecology Research, 2*(4), 493–508.

Bleu, J., Bessa-Gomes, C., & Laloi, D. (2012). Evolution of female choosiness and mating frequency: effects of mating cost, density and sex ratio. *Animal Behaviour, 83*(1), 131–136. http://dx.doi.org/10.1016/j.anbehav.2011.10.017.

Bogacz, R., Brown, E., Moehlis, J., Holmes, P., & Cohen, J. D. (2006). The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. *Psychological Review, 113*(4), 700–765. http://dx.doi.org/10.1037/0033-295X.113.4.700.

Bonachea, L. A., & Ryan, M. J. (2011). Localization error and search costs during mate choice in túngara frogs, *Physalaemus pustulosus*. *Ethology, 117*(1), 56–62. http://dx.doi.org/10.1111/j.1439-0310.2010.01843.x.

Booksmythe, I., Detto, T., & Backwell, P. R. Y. (2008). Female fiddler crabs settle for less: the travel costs of mate choice. *Animal Behaviour, 76*(6), 1775–1781. http://dx.doi.org/10.1016/j.anbehav.2008.07.022.

Breedveld, M. C., & Fitze, P. S. (2015). A matter of time: delayed mate encounter postpones mating window initiation and reduces the strength of female choosiness. *Behavioral Ecology and Sociobiology, 69*(4), 533–541. http://dx.doi.org/10.1007/s00265-014-1864-y.

Byers, J. A., Wiseman, P. A., Jones, L., & Roffe, T. J. (2005). A large cost of female mate sampling in Pronghorn. *American Naturalist, 166*(6), 661–668. http://dx.doi.org/10.1086/497401.

Byers, J. A., Byers, A. A., & Dunn, S. J. (2006). A dry summer diminishes mate search effort by pronghorn females: evidence for a significant cost of mate search. *Ethology, 112*, 74–80. http://dx.doi.org/10.1007/s00442-014-3124-2.

Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews, 78*(4), 575–595. http://dx.doi.org/10.1017/S1464793103006158.

Castellano, S. (2009a). Towards an information-processing theory of mate choice. *Animal Behaviour, 78*(6), 1493–1497. http://dx.doi.org/10.1016/j.anbehav.2009.10.002.

Castellano, S. (2009b). Unreliable preferences, reliable choice and sexual selection in leks. *Animal Behaviour, 77*(1), 225–232. http://dx.doi.org/10.1016/j.anbehav.2008.09.017.

Castellano, S., Cadeddu, G., & Cermelli, P. (2012). Computational mate choice: theory and empirical evidence. *Behavioural Processes, 90*(2), 261–277. http://dx.doi.org/10.1016/j.beproc.2012.02.010.

Castellano, S., & Cermelli, P. (2011). Sampling and assessment accuracy in mate choice: a random-walk model of information processing in mating decision. *Journal of Theoretical Biology, 274*(1), 161–169. http://dx.doi.org/10.1016/j.jtbi.2011.01.001.

Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology and Evolution, 24*(7), 400–407. http://dx.doi.org/10.1016/j.tree.2009.02.010.

Collins, E. J., & McNamara, J. M. (1993). The job-search problem with competition: an evolutionarily stable dynamic strategy. *Advances in Applied Probability, 25*(2), 314–333. http://dx.doi.org/10.2307/1427655.

Collins, E. J., McNamara, J. M., & Ramsey, D. M. (2006). Learning rules for optimal selection in a varying environment: mate choice revisited. *Behavioral Ecology, 17*(5), 799–809. http://dx.doi.org/10.1093/beheco/arl008.

Cotton, S., Small, J., & Pomiankowski, A. (2006). Sexual selection and condition-dependent mate preferences. *Current Biology, 16*(17), R755–R765. http://dx.doi.org/10.1016/j.cub.2006.08.022.

Dale, S., Amundsen, T., Lifjeld, J. T., & Slagsvold, T. (1990). Mate sampling behaviour of female pied flycatchers: evidence for active mate choice. *Behavioral Ecology and Sociobiology, 27*(2). http://dx.doi.org/10.2307/4600449.

De Jong, M. C. M., & Sabelis, M. W. (1991). Limits to runaway sexual selection: the wallflower paradox. *Journal of Evolutionary Biology, 4*(4), 637–655. http://dx.doi.org/10.1046/j.1420-9101.1991.4040637.x.

Dechaume-Moncharmont, F.-X., Freychet, M., Motreuil, S., & Cézilly, F. (2013). Female mate choice in convict cichlids is transitive and consistent with a self-referent directional preference. *Frontiers in Zoology, 10*(1), 69. http://dx.doi.org/10.1186/1742-9994-10-69.

Dombrovsky, Y., & Perrin, N. (1994). On adaptive search and optimal stopping in sequential mate choice. *American Naturalist, 144*(2). http://dx.doi.org/10.2307/2463166.

Donald, P. F. (2007). Adult sex ratios in wild bird populations. *Ibis, 149*(4), 671–692. http://dx.doi.org/10.1111/j.1474-919x.2007.00724.x.

Dukas, R., & Baxter, C. M. (2014). Mate choosiness in young male fruit flies. *Behavioral Ecology, 25*(3), 549–552. http://dx.doi.org/10.1093/beheco/aru020.

Dunn, P. O., Winkler, D. W., Whittingham, L. A., Hannon, S. J., & Robertson, R. J. (2011). A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore? *Ecology, 92*(2), 450–461. http://dx.doi.org/10.1890/10-0478.1.

Etienne, L., Rousset, F., Godelle, B., & Courtiol, A. (2014). How choosy should I be? The relative searching time predicts evolution of choosiness under direct sexual selection. *Proceedings of the Royal Society B: Biological Sciences, 281*(1785), 20140190.

Fawcett, T. W., & Bleay, C. (2009). Previous experiences shape adaptive mate preferences. *Behavioral Ecology, 20*(1), 68–78. http://dx.doi.org/10.1093/beheco/arn116.

Fawcett, T. W., Fallenstein, B., Higginson, A. D., Houston, A. I., Mallpress, D. E. W., Trimmer, P. C., et al. (2014). The evolution of decision rules in complex environments. *Trends in Cognitive Sciences, 18*(3), 153–161. http://dx.doi.org/10.1016/j.tics.2013.12.012.

Fawcett, T. W., & Johnstone, R. A. (2003). Mate choice in the face of costly competition. *Behavioral Ecology, 14*(6), 771–779. http://dx.doi.org/10.1093/beheco/arg075.

Ferguson, T. S. (1989). Who solved the secretary problem? *Statistical Science, 4*(3), 282–289. Retrieved from http://www.jstor.org/stable/2245639.

Fiske, P., & Kalas, J. A. (1995). Mate sampling and copulation behaviour of great snipe females. *Animal Behaviour, 49*(1), 209–219. http://dx.doi.org/10.1016/0003-3472(95)80169-3.

Friedl, T. W. P., & Klump, G. M. (2005). Sexual selection in the lek-breeding European treefrog: body size, chorus attendance, random mating and good genes. *Animal Behaviour, 70*(5), 1141–1154. http://dx.doi.org/10.1016/j.anbehav.2005.01.017.

Gibson, R. M. (1996). Female choice in sage grouse: the roles of attraction and active comparison. *Behavioral Ecology and Sociobiology, 39*(1), 55–59. http://dx.doi.org/10.1007/s002650050266.

Godin, J.-G. J., & Briggs, S. E. (1996). Female mate choice under predation risk in the guppy. *Animal Behaviour, 51*(1), 117–130. http://dx.doi.org/10.1006/anbe.1996.0010.

Härdling, R., & Kokko, H. (2005). The evolution of prudent choice. *Evolutionary Ecology Research, 7*, 697–715.

Hereford, J., Hansen, T. F., & Houle, D. (2004). Comparing strengths of directional selection: how strong is strong? *Evolution, 58*(10), 2133–2143. Retrieved from http://view.ncbi.nlm.nih.gov/pubmed/15562680.

Heuschele, J., Mannerla, M., Gienapp, P., & Candolin, U. (2009). Environment-dependent use of mate choice cues in sticklebacks. *Behavioral Ecology, 20*(6), 1223–1227. http://dx.doi.org/10.1093/beheco/arp123.

Houston, A. I. (1997). Natural selection and context-dependent values. *Proceedings of the Royal Society B: Biological Sciences, 264*(1387), 1539–1541. http://dx.doi.org/10.1098/rspb.1997.0213.

Houston, A. I., & McNamara, J. M. (2002). A self-consistent approach to paternity and parental effort. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 357*(1419), 351–362. http://dx.doi.org/10.1098/rstb.2001.0925.

Janetos, A. C. (1980). Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology, 7*(2), 107–112. http://dx.doi.org/10.1007/BF00299515.

Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews, 72*(02), 283–327.

Jennions, M. D., & Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. *Biological Reviews, 75*(1), 21–64. http://dx.doi.org/10.1111/j.1469-185X.1999.tb00040.x.

Johnstone, R. A. (1997). The tactics of mutual mate choice and competitive search. *Behavioral Ecology and Sociobiology, 40*(1), 51–59. http://dx.doi.org/10.1007/s002650050315.

Johnstone, R. A., Reynolds, J. D., & Deutsch, J. C. (1996). Mutual mate choice and sex differences in choosiness. *Evolution, 50*(4), 1382–1391. Retrieved from http://www.jstor.org/stable/2410876.

Kacelnik, A. (2006). Meanings of rationality. In S. Hurley, & M. Nudds (Eds.), *Rational animals?* (pp. 87–105). Oxford, U.K.: Oxford University Press. Retrieved from http://www.amazon.com/Rational-Animals-Susan-Hurley/dp/0198528272.

Kodric-Brown, A., & Nicoletto, P. F. (2001). Age and experience affect female choice in the guppy (*Poecilia reticulata*). *American Naturalist, 157*(3), 316–323. http://dx.doi.org/10.1086/319191.

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology, 68*(5), 940–950. http://dx.doi.org/10.1046/j.1365-2656.1999.00343.x.

Kokko, H., Booksmythe, I., & Jennions, M. D. (2014). Mate-sampling costs and sexy sons. *Journal of Evolutionary Biology, 28*(1), 259–266. http://dx.doi.org/10.1111/jeb.12532.

Kokko, H., & Mappes, J. (2005). Sexual selection when fertilization is not guaranteed. *Evolution, 59*(9), 1876–1885. http://dx.doi.org/10.1111/j.0014-3820.2005.tb01058.x.

Kokko, H., & Ots, I. (2006). When not to avoid inbreeding. *Evolution, 60*(3), 467–475. http://dx.doi.org/10.1111/j.0014-3820.2006.tb01128.x.

Kokko, H., & Wong, B. B. M. (2007). What determines sex roles in mate searching? *Evolution, 61*(5), 1162–1175. http://dx.doi.org/10.1111/j.1558-5646.2007.00090.x.

Kosztolányi, A., Barta, Z., Küpper, C., & Székely, T. (2011). Persistence of an extreme male-biased adult sex ratio in a natural population of polyandrous bird. *Journal of Evolutionary Biology, 24*(8), 1842–1846. http://dx.doi.org/10.1111/j.1420-9101.2011.02305.x.

Kuijper, B., Pen, I., & Weissing, F. J. (2012). A guide to sexual selection theory. *Annual Review of Ecology, Evolution, and Systematics, 43*(1), 311. http://dx.doi.org/10.1146/annurev-ecolsys-110411-160245.

Kvarnemo, C., & Ahnesjö, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology and Evolution, 11*(10), 404–408. http://dx.doi.org/10.1016/0169-5347(96)10056-2.

Kvarnemo, C., & Simmons, L. W. (1999). Variance in female quality, operational sex ratio and male mate choice in a bushcricket. *Behavioral Ecology and Sociobiology, 45*(3–4), 245–252. http://dx.doi.org/10.1007/s002650050559.

Lea, J., Halliday, T., & Dyson, M. (2000). Reproductive stage and history affect the phonotactic preferences of female midwife toads, *Alytes muletensis*. *Animal Behaviour, 60*(4), 423–427. http://dx.doi.org/10.1006/anbe.2000.1482.

Lea, A. M., & Ryan, M. J. (2015). Irrationality in mate choice revealed by túngara frogs. *Science, 349*(6251), 964–966. http://dx.doi.org/10.1126/science.aab2012.

Leonard, A. S., & Hedrick, A. V. (2009). Male and female crickets use different decision rules in response to mating signals. *Behavioral Ecology, 20*(6), 1175–1184. http://dx.doi.org/10.1093/beheco/arp115.

Lindström, K., & Lehtonen, T. K. (2013). Mate sampling and choosiness in the sand goby. *Proceedings of the Royal Society B: Biological Sciences, 280*(1765), 20130983. http://dx.doi.org/10.1098/rspb.2013.0983.

Luttbeg, B. (1996). A comparative Bayes tactic for mate assessment and choice. *Behavioral Ecology, 7*(4), 451–460. http://dx.doi.org/10.1093/beheco/7.4.451.

Luttbeg, B. (2004). Female mate assessment and choice behavior affect the frequency of alternative male mating tactics. *Behavioral Ecology, 15*(2), 239–247. http://dx.doi.org/10.1093/beheco/arh002.

Lynch, K. S., Stanely Rand, A., Ryan, M. J., & Wilczynski, W. (2005). Plasticity in female mate choice associated with changing reproductive states. *Animal Behaviour, 69*(3), 689–699. http://dx.doi.org/10.1016/j.anbehav.2004.05.016.

Madden, J. R., & Whiteside, M. A. (2013). Variation in female mate choice and mating success is affected by sex ratio experienced during early life. *Animal Behaviour*. http://dx.doi.org/10.1016/j.anbehav.2013.05.003.

Mangel, M., & Clark, C. W. (1988). *Dynamic modeling in behavioral ecology*. Princeton, NJ: Princeton University Press. Retrieved from http://www.worldcat.org/isbn/0691085064.

Mazalov, V., Perrin, N., & Dombrovsky, Y. (1996). Adaptive search and information updating in sequential mate choice. *American Naturalist, 148*(1). http://dx.doi.org/10.2307/2463074.

McCall, B. P., & McCall, J. J. (2008). *The economics of search*. London, U.K.: Routledge. Retrieved from http://www.amazon.com/exec/obidos/redirect?tag=citeulike07-20&path=ASIN/0415299926.

McLean, M. J., Bishop, P. J., & Nakagawa, S. (2012). Male quality, signal reliability and female choice: assessing the expectations of inter-sexual selection. *Journal of Evolutionary Biology, 25*(8), 1513–1520. http://dx.doi.org/10.1111/j.1420-9101.2012.02533.x.

McNamara, J. M. (2013). Towards a richer evolutionary game theory. *Journal of the Royal Society Interface, 10*(88), 20130544. http://dx.doi.org/10.1098/rsif.2013.0544.

McNamara, J. M., & Fawcett, T. W. (2012). Optimal strategies and heuristics for ecological search problems. In P. M. Todd, T. T. Hills, & T. W. Robbins (Eds.), *Cognitive search: Evolution, algorithms, and the brain* (pp. 301–315). Cambridge, MA: MIT Press.

McNamara, J. M., Webb, J. N., Collins, E. J., Székely, T., & Houston, A. I. (1997). A general technique for computing evolutionarily stable strategies based on errors in decision-making. *Journal of Theoretical Biology, 189*(2), 211–225. http://dx.doi.org/10.1006/jtbi.1997.0511.

Meuche, I., Brusa, O., Linsenmair, K., Keller, A., & Prohl, H. (2013). Only distance matters – non-choosy females in a poison frog population. *Frontiers in Zoology, 10*(1), 29. http://dx.doi.org/10.1186/1742-9994-10-29.

Milinski, M., & Bakker, T. C. M. (1992). Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. *Proceedings of the Royal Society B: Biological Sciences, 250*(1329), 229–233. http://dx.doi.org/10.1098/rspb.1992.0153.

Mohamad, R., Wajnberg, E., Monge, J.-P., & Goubault, M. (2015). The effect of direct interspecific competition on patch exploitation strategies in parasitoid wasps. *Oecologia, 177*, 305–315. http://dx.doi.org/10.1007/s00442-014-3124-2.

Moore, A. J., & Moore, P. J. (1988). Female strategy during mate choice: threshold assessment. *Evolution, 42*(2), 387–391. Retrieved from http://www.jstor.org/stable/2409241.

Moore, P. J., & Moore, A. J. (2001). Reproductive aging and mating: the ticking of the biological clock in female cockroaches. *Proceedings of the National Academy of Sciences, 98*(16), 9171–9176. http://dx.doi.org/10.1073/pnas.161154598.

Murphy, C. G., & Gerhardt, H. C. (2002). Mate sampling by female barking treefrogs (*Hyla gratiosa*). *Behavioral Ecology, 13*(4), 472–480. http://dx.doi.org/10.1093/beheco/13.4.472.

Parker, G. A. (1983). Mate quality and mating decisions. In P. Bateson (Ed.), *Mate choice* (pp. 141–166). Cambridge, U.K.: Cambridge University Press.

Phelps, S. M., Rand, A. S., & Ryan, M. J. (2006). A cognitive framework for mate choice and species recognition. *American Naturalist, 167*(1), 28–42.

Poethke, H. J., & Hovestadt, T. (2002). Evolution of density–and patch–size–dependent dispersal rates. *Proceedings of the Royal Society B: Biological Sciences, 269*(1491), 637–645. http://dx.doi.org/10.1098/rspb.2001.1936.

Pomiankowski, A. (1987). The costs of choice in sexual selection. *Journal of Theoretical Biology, 128*(2), 195–218. http://dx.doi.org/10.1016/s0022-5193(87)80169-8.

R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria. Retrieved from http://www.r-project.org/.

Ramsey, D. M. (2008). A large population job search game with discrete time. *European Journal of Operational Research, 188*(2), 586–602. http://dx.doi.org/10.1016/j.ejor.2007.05.031.

Ramsey, D. M. (2011). Mutual mate choice with multiple criteria. In M. Breton, & K. Szajowski (Eds.), *Advances in dynamic games* (Vol. 11, pp. 337–355). Boston, MA: Birkhäuser. http://dx.doi.org/10.1007/978-0-8176-8089-3_17.

Real, L. A. (1990). Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist, 136*(3), 376–405. http://dx.doi.org/10.2307/2462150.

Real, L. A. (1991). Search theory and mate choice. II. Mutual interaction, assortative mating, and equilibrium variation in male and female fitness. *American Naturalist, 138*(4). http://dx.doi.org/10.2307/2462440.

Reinhold, K., & Schielzeth, H. (2014). Choosiness, a neglected aspect of preference functions: a review of methods, challenges and statistical approaches. *Journal of Comparative Physiology A, 201*(1), 171–182. http://dx.doi.org/10.1007/s00359-014-0963-6.

Roff, D. A. (2015). The evolution of mate choice: a dialogue between theory and experiment. *Annals of the New York Academy of Sciences, 1360*(1), 1–15. http://dx.doi.org/10.1111/nyas.12743.

Rosvall, K. A. (2011). Intrasexual competition in females: evidence for sexual selection? *Behavioral Ecology, 22*(6), 1131–1140. http://dx.doi.org/10.1093/beheco/arr106.

Rowell, J. T., & Servedio, M. R. (2009). Gentlemen prefer blondes: the evolution of mate preference among strategically allocated males. *American Naturalist, 173*(1), 12–25. http://dx.doi.org/10.1086/593356.

Rundus, A. S., Sullivan-Beckers, L., Wilgers, D. J., & Hebets, E. A. (2011). Females are choosier in the dark: environment-dependent reliance on courtship components and its impact on fitness. *Evolution, 65*(1), 268–282. http://dx.doi.org/10.1111/j.1558-5646.2010.01125.x.

Schacht, R., & Borgerhoff Mulder, M. (2015). Sex ratio effects on reproductive strategies in humans. *Royal Society Open Science, 2*(1), 140402. http://dx.doi.org/10.1098/rsos.140402.

Scheutz, M., Harris, J., & Boyd, S. K. (2010). How to pick the right one: investigating tradeoffs among female mate choice strategies in treefrogs. In S. Doncieux, B. Girard, A. Guillot, J. Hallam, J.-A. Meyer, & J.-B. Mouret (Eds.), *From animals to animats 11* (Vol. 6226, pp. 618–627). Berlin, Germany: Springer Verlag. http://dx.doi.org/10.1007/978-3-642-15193-4_58.

Seale, D. A., & Rapoport, A. (1997). Sequential decision making with relative ranks: an experimental investigation of the 'secretary problem'. *Organizational Behavior and Human Decision Processes, 69*(3), 221–236. http://dx.doi.org/10.1006/obhd.1997.2683.

Seale, D. A., & Rapoport, A. (2000). Optimal stopping behavior with relative ranks: the secretary problem with unknown population size. *Journal of Behavioral Decision Making, 13*(4), 391–411. http://dx.doi.org/10.1002/1099-0771(200010/12)13:4\%3C391::aid-bdm359\%3E3.0.co;2-i.

Seubert, S. M., Wade, G. A., & Wiegmann, D. D. (2011). The variability of male quality and female mate choice decisions: second-order stochastic dominance and the behavior of searchers under a sequential search strategy. *Journal of Mathematical Biology, 63*(6), 1121–1138. http://dx.doi.org/10.1007/s00285-010-0399-8.

Stein, W. E., Seale, D. A., & Rapoport, A. (2003). Analysis of heuristic solutions to the best choice problem. *European Journal of Operational Research, 151*(1), 140–152. http://dx.doi.org/10.1016/S0377-2217(02)00601-X.

Stoffer, B., & Uetz, G. W. (2015). The effects of social experience with varying male availability on female mate preferences in a wolf spider. *Behavioral Ecology and Sociobiology, 69*(6), 927–937. http://dx.doi.org/10.1007/s00265-015-1904-2.

Todd, P. M., & Gigerenzer, G. (2012). *Ecological rationality: Intelligence in the world.* Oxford, U.K.: Oxford University Press.

Trail, P. W., & Adams, E. S. (1989). Active mate choice at cock-of-the-rock leks: tactics of sampling and comparison. *Behavioral Ecology and Sociobiology, 25*(4), 283–292. http://dx.doi.org/10.1007/BF00300055.

Trimmer, P. C., Houston, A. I., Marshall, J. A. R., Bogacz, R., Paul, E. S., Mendl, M. T., et al. (2008). Mammalian choices: combining fast-but-inaccurate and slow-but-accurate decision-making systems. *Proceedings of the Royal Society B: Biological Sciences, 275*(1649), 2353–2361. http://dx.doi.org/10.1098/rspb.2008.0417.

Uy, J. A. C., Patricelli, G. L., & Borgia, G. (2001). Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *American Naturalist, 158*(5), 530–542. http://dx.doi.org/10.1086/323118.

Valone, T. J., Nordell, S. E., Giraldeau, L.-A., & Templeton, J. J. (1996). The empirical question of thresholds and mechanisms of mate choice. *Evolutionary Ecology, 10*(4), 447–455. http://dx.doi.org/10.1007/BF01237729.

Venner, S., Bernstein, C., Dray, S., & Bel-Venner, M.-C. (2010). Make love not war: when should less competitive males choose low-quality but defendable females? *American Naturalist, 175*(6), 1–14. http://dx.doi.org/10.1086/652432.

Wagner, W. E. (1998). Measuring female mating preferences. *Animal Behaviour, 55*(4), 1029–1042. http://dx.doi.org/10.1006/anbe.1997.0635.

Widemo, F., & Sæther, S. A. (1999). Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends in Ecology and Evolution, 14*(1), 26–31. http://dx.doi.org/10.1016/S0169-5347(98)01531-6.

Wiegmann, D. D., & Angeloni, L. M. (2007). Mate choice and uncertainty in the decision process. *Journal of Theoretical Biology, 249*(4), 654–666. http://dx.doi.org/10.1016/j.jtbi.2007.08.027.

Wiegmann, D. D., Angeloni, L. M., Seubert, S. M., & Wade, J. G. (2013). Mate choice decisions by searchers. *Current Zoology, 59*(2), 184–1999.

Wiegmann, D. D., Mukhopadhyay, K., & Real, L. A. (1999). Sequential search and the influence of male quality on female mating decisions. *Journal of Mathematical Biology, 39*(3), 193–216. http://dx.doi.org/10.1007/s002850050168.

Wiegmann, D. D., Real, L. A., Capone, T. A., & Ellner, S. (1996). Some distinguishing features of models of search behavior and mate choice. *American Naturalist, 147*(2). http://dx.doi.org/10.2307/2463201.

Wiegmann, D. D., Seubert, S. M., & Wade, G. A. (2010). Mate choice and optimal search behavior: fitness returns under the fixed sample and sequential search strategies. *Journal of Theoretical Biology, 262*(4), 596–600. http://dx.doi.org/10.1016/j.jtbi.2009.08.033.

Willis, P. M., Ryan, M. J., & Rosenthal, G. G. (2011). Encounter rates with conspecific males influence female mate choice in a naturally hybridizing fish. *Behavioral Ecology, 22*(6), 1234–1240. http://dx.doi.org/10.1093/beheco/arr119.

Wittenberger, J. F. (1983). Tactics of mate choice. In P. Bateson (Ed.), *Mate choice* (pp. 435–447). Cambridge, U.K.: Cambridge University Press.

Wong, B. B. M., & Candolin, U. (2005). How is female mate choice affected by male competition? *Biological Reviews, 80*(4), 559–571. http://dx.doi.org/10.1017/S1464793105006809.

## APPENDIX: SENSITIVITY ANALYSIS: EFFECT OF THE MEAN MALE QUALITY.

Following Janetos (1980), as default values, the male's quality was normally distributed ($\mu = 10$, $\sigma = 1$). With these parameters, pairing with one of the males from the lowest quantile of the quality distribution was still far better than no reproduction at all. As the fitness can be understood as a relative measure, changing the distribution parameters of male quality had generally no effects on the ESS. However, in the case of large variance or low mean quality, the distribution of male quality was truncated in order to avoid negative fitness gain for the female: each negative fitness gain was reduced to a null fitness, which corresponds to the pairing with a sterile male. When the mean quality decreased while the variance remained constant (i.e. when the relative difference between the best and worst male increased while their absolute difference remained constant), the proportion of low-quality males leading to a truncated fitness increased (Fig. A1a). The ESS threshold criterion thus increased, but this increase corresponds to a modification of the operational sex ratio as the number of fertile males decreased (Fig. A1b). This effect became apparent for a proportion of sterile males larger than a few per cent (for instance, with $\mu = 2$, 2.2% of the males were sterile on average). The best-of-$n$ decision rule was less sensitive than the threshold decision rule to the modification of the distribution parameters (Fig. A1c). This was expected because it is a comparative rule based on rank. The fact that the lowest quality males within the fixed sample led to a poor (eventually null) fitness gain had no serious consequences for the decision rule.
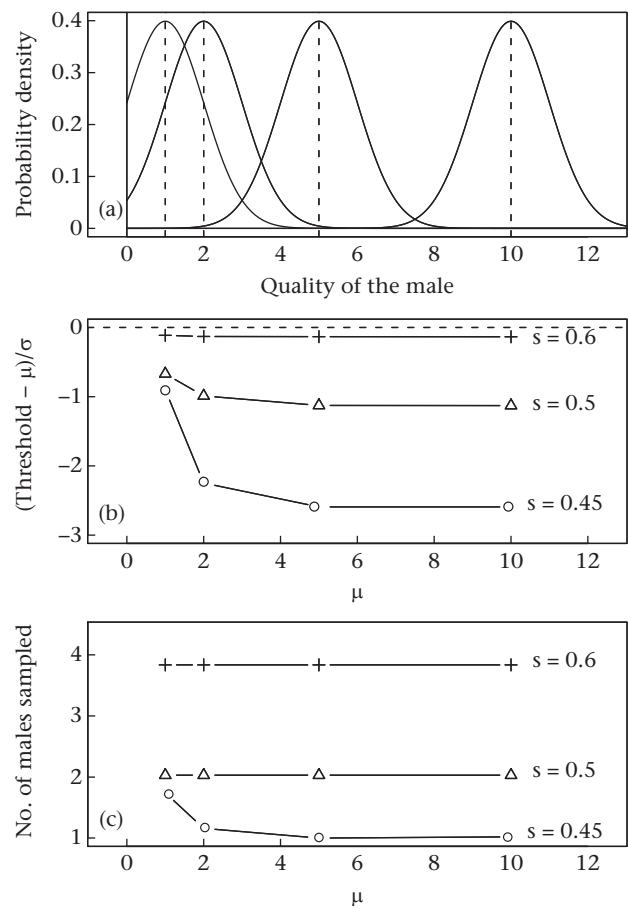


**Fig. A1.** Comparison of ESS choosiness as a function of the mean male quality. (a) Probability density function of male quality for four populations centred around either $\mu = 1$, $\mu = 2$, $\mu = 5$ or $\mu = 10$. The standard deviation was kept constant, $\sigma = 1$. With $\mu = 2$, 2.2% of the males were expected to have a quality truncated at zero (a female would have no fitness gain to mate with these males). With $\mu = 1$, this percentage was 16%. (b) ESS for the threshold decision rule with the last-chance option for three proportions of males: $s = 0.45$ (circle), 0.5 (triangle) and 0.6 (cross). Because the threshold criterion is defined as an absolute value of quality, it is expected to decrease with $\mu$. To compare the ESS criteria across the condition, they have been shown as standardized values $(w_c{}^* - \mu)/\sigma$, which represents a distance (in standard deviation units) to the mean male quality. (c) ESS for the best-of-$n$ decision rule. The sex ratio and key are the same as in (b).