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

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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.
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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

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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 α 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 α 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