

# Fluctuating Dynamics of Mate Availability Promote the Evolution of Flexible Choosiness in Both Sexes

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**ABSTRACT:** The evolution of choosiness has a strong effect on sexual selection, as it promotes variance in mating success among individuals. The context in which choosiness is expressed, and therefore the associated gain and cost, is highly variable. An overlooked mechanism by current models is the rapid fluctuations in the availability and quality of partners, which generates a dynamic mating market to which each individual must optimally respond. We argue that the rapid fluctuations of the mating market are central to the evolution of optimal choosiness. Using a dynamic game approach, we investigate this hypothesis for various mating systems (characterized by different adult sex ratio and latency period combinations), allowing feedback between the choosiness and partner availability throughout a breeding season while taking into account the fine variation in individual quality. Our results indicate that quality-dependent and flexible choosiness usually evolve in both sexes for various mating systems and that a significant amount of variance in choosiness is observed, especially in males, even when courtship is costly. Accounting for the fluctuating dynamics of the mating market therefore allows envisioning a much wider range of choosiness variation in natural populations and may explain a number of recent empirical results regarding choosiness in the less common sex or its variance within sexes.

**Keywords:** choosiness, mutual mate choice, flexibility, context dependency, game theory, scramble competition.

## Introduction

In most animal species, individuals mate preferentially with some individuals over others, thereby displaying a choosy behavior. Choosiness can be defined as the probability that an encountered individual of a given quality

is considered an appropriate mate and is therefore accepted rather than rejected. Understanding the evolution of choosiness and underlying rules is paramount to understanding sexual selection, because mate choice leads to interindividual variability in reproductive success in the chosen sex (Darwin 1871; Andersson 1994; Jennions and Petrie 1997). The evolution of mate choice has been shown to depend on different factors. Optimal choosiness is predicted to increase: (i) when the survival cost of mate searching (or attraction) decreases (Real 1990; Crowley et al. 1991; Kokko and Johnstone 2002; Kopp and Hermisson 2008), (ii) when the costs of mating associated with lower survival when breeding becomes greater (Kokko and Monaghan 2001; Kokko and Johnstone 2002; Kopp and Hermisson 2008; Bleu et al. 2011), (iii) with increasing variance in mate quality in the population (Real 1990; Owens and Thompson 1994; Johnstone et al. 1996; Kokko and Johnstone 2002), or (iv) when mate availability increases as the risk of not finding an alternative mate decreases (Bleu et al. 2011; Fawcett et al. 2011; Etienne et al. 2014; Courtiol et al. 2016; Dechaume-Moncharmont et al. 2016).

Most of these factors are characteristics of the population and can therefore be considered constant on a relatively short timescale, such that their effect on choosiness should be significant across rather than within generations. For instance, the mating rate of individuals will be restricted by a period of unavailability after mating, dedicated to the replenishment of the gametic stock or to parental care, hereafter called the latency period, which will depend mainly on the physiology of the species. When factors affecting mate choice are constant, models predict that the evolution of mutual mate choice should only be observed under a restrictive set of conditions, specifically when latency periods are long and equal between sexes (thus the breeding cost is high) and when adult sex ratio (ASR) at maturation is balanced (Kokko and Johnstone

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2002; Kokko and Jennions 2008; Fromhage and Jennions 2016). When population characteristics depart from such specific conditions (e.g., owing to different latency periods between sexes, unbalanced ASR, or unbalanced maturation sex ratio because of differences in mortality between sexes), choosiness is usually favored in the less common sex. The expected differences in choosiness between the sexes can be amplified by a mechanism at the center of some previous models: the increase in choosiness in one sex is expected to cause a decrease in its mating rate, which also mechanically reduces the mating rate in the other sex, in which the choice therefore becomes even less favored (Kokko and Johnstone 2002; Courtiol et al. 2016). Importantly, the reduction in the mating rate associated with choosiness (i.e., the opportunity cost; Fawcett et al. 2011; Etienne et al. 2014; Dechaume-Moncharmont et al. 2016) can vary within generations and among individuals too. In particular, the number and quality distribution of mates available to a focal individual may change drastically among individuals and over time. Indeed, individuals who differ in their attractiveness may also vary in the number and average quality of mating partners they get access to (Johnstone 1997; McNamara et al. 1997). Rather than depending on fixed and homogeneous strategies, mating can be context dependent (Fricke et al. 2009; Rowe and Arnqvist 2015; Gauthey et al. 2016) and is therefore likely the result of a complex dynamic game where each individual tries at any time to maximize its reproductive output by optimizing its choosiness with regard to the choosiness of its competitors (Johnstone 1997; Fawcett and Johnstone 2003; Alpern and Reyniers 2005; Gowaty and Hubbell 2009; Bleu et al. 2011; Ramsey 2011). Of great interest is the possibility that choosiness evolves in both sexes, thereby giving rise to mutual mate choice, adding a new dimension in the game wherein individuals have to adjust not only to the choosiness of their same-sex competitors but also to the change in choosiness of the opposite sex (McNamara and Collins 1990; Collins and McNamara 1993; Johnstone 1997; Kokko and Monaghan 2001; Kokko and Johnstone 2002; Alpern and Reyniers 2005; Ramsey 2011; Courtiol et al. 2016). There are now several experimental publications suggesting that individuals can respond to such fluctuations by flexibly modifying their selection criteria (Chaine and Lyon 2008; Bailey and Zuk 2009; Tinghitella et al. 2013).

Finally, different mating systems, characterized for instance by contrasted ASR or differences in latency periods between sexes, can influence the dynamics with regard to the availability of mating partners (both in quantity and quality). This will in turn strongly affect the mating market, making optimal choosiness between sexes, between quality, and over time a nontrivial pattern. An associated yet central benefit of considering quality- and time-dependent choosiness is to bolster interactions be-

tween theoretical and empirical research: experiments and most observations in natural environments involve complex situations where individuals interact in a fluctuating context, producing choosiness that changes over time, or with the quality or sex of the individual (Byrne and Rice 2006; Labonne et al. 2009; Judge et al. 2014). This potentially generates variation in choosiness that is not necessarily captured by the current theoretical models. We argue that the existence of such variation is a fertile ground to improve our understanding of choosiness evolution and should therefore be accounted for in predictive models. To that end, we here present a dynamic game-theoretical model explicitly accounting for fluctuations in mate availability over a finite breeding season, where individuals of both sexes and of different quality can flexibly change their choosiness as a response to those fluctuations. Although we apply our model to a large range of mating systems and competitive conditions, we focus specifically on a polygynandrous mating system to demonstrate the complex relationship between the mating market dynamics, the evolution of quality-dependent and flexible choosiness, and the resulting patterns of mate choice.

## Methods

### *The Game Model*

The model is formulated as a dynamic game that describes mating in a population of females and males of different qualities. Both sexes are potentially choosy. All individuals have the possibility to compete for partners of variable quality. As a consequence, their fitness payoffs also depend on the choices made by the other individuals from both sexes in the population. We build a discrete time model with a finite time horizon (i.e., the breeding season) of length  $T$  time steps. Each individual is characterized by its quality (denoted  $q$ ), which is a discrete value among  $Q = 100$  possible classes of qualities regularly spaced between 0 and 1. The lowest class, noted  $q = 0$ , corresponds to the interval of quality  $[0, 0.01]$  and the highest class, noted  $q = 100$ , corresponds to the interval of quality  $[0.99, 1]$ . Individual quality remains constant over the breeding season. We here assume that the fitness payoff from mating for an individual depends only on the quality of its mate or mates (but we also explored a fitness payoff equal to the product of qualities between partners; supplement 5; supplements 1–5 are available online). Initially,  $f(q)$  specifies the probability distribution of individuals of quality for both males and females. The notations  $f(q, t)_{\delta}$  and  $f(q, t)_{\phi}$ , respectively, are the relative frequency of males of quality  $q$  among available males and the relative frequency of females of quality  $q$  among available females, at time  $t$ . The model describes a mate encounter process

wherein, at each time step, individuals have a probability of encountering an available partner of a given quality (i.e., mass encounter; Gimelfarb 1988). When they meet, individuals independently and immediately (within the time step of the encounter) decide whether they accept mating or not. At a given time step  $t$ , when courtship is costless, their choice depends on their own quality and the quality of the encountered partner, as well as on the quality of prospective partners they could expect to meet before the end of the breeding season. Therefore, the model implicitly assumes that individuals know the opposite-sex distribution of quality throughout the breeding season. The choosiness strategy for an individual of quality  $q$ , denoted  $p_{\delta}(q, q', t)$  for males and  $p_{\varphi}(q, q', t)$  for females, is therefore a  $Q \times Q \times T$  matrix of acceptance probabilities for every possible partner's quality  $q'$  and at each time step  $t$ . Mated individuals become unavailable for further mating during their latency period, denoted  $\tau_{\delta}$  for males and  $\tau_{\varphi}$  for females. At the end of their latency, they return to the pool of available partners. When  $\tau_{\delta}$  and  $\tau_{\varphi}$  are greater than the length of the breeding season, each individual can only expect to mate once during the breeding season, which corresponds to a case of monogamy. Other mating systems are modeled as follows: polygyny ( $\tau_{\delta} \ll T$  and  $\tau_{\varphi} \gg T$ ), polyandry ( $\tau_{\varphi} \ll T$  and  $\tau_{\delta} \gg T$ ), or polygynandry ( $\tau_{\delta} \ll T$  and  $\tau_{\varphi} \ll T$ ). Contrary to the ASR, which is the initial sex ratio of mature individuals in the population and is defined only at the beginning of the breeding season, the operational sex ratio( $t$ ), or OSR( $t$ ), is the ratio of available males to available females and changes dynamically during the breeding season, depending on latency periods, ASR, and the dynamics of the market. The OSR and the distribution of unpaired individual qualities are therefore emergent properties of the pair formation process, which results from choosiness strategies in the population.

#### Evolutionarily Stable Strategy of Choosiness

The reproductive success of an individual depends on the strategies of other players through direct interactions between encountered partners (because the choice is mutual) or indirect interactions between competitors via the removal of available partners in the population. To calculate the evolutionarily stable strategy, we used a method of best response iterations (Houston and McNamara 1999; Roff 2010). The core of the optimization algorithm is a two-step process. We begin with an arbitrary set of choice strategies,  $p_{\text{resident}\delta}(q, q', t)$  and  $p_{\text{resident}\varphi}(q, q', t)$  and, for each time step  $t$ , we calculate the distributions of qualities for males ( $f_{\delta}(q, t)$ ) and females ( $f_{\varphi}(q, t)$ ) that result from this set of strategies (app. A, available online). Assuming these distributions of quality, we then calculate the best response strategies for

both sexes,  $p_{\text{best}\delta}(q, q', t)$  and  $p_{\text{best}\varphi}(q, q', t)$ , as the strategies that maximize the individual's expected payoffs (see details below). The new resident set of strategies to be used in the next iteration is derived from the previous one as follows:

$$p_{\text{new}\delta}(q, q', t) = (1 - \lambda)p_{\text{resident}\delta}(q, q', t) + \lambda p_{\text{best}\delta}(q, q', t), \quad (1)$$

where  $\lambda$  is a damping term that prevents oscillations in the iterative calculation of the optimal strategy (McNamara et al. 1997). This new set of strategies is used to calculate the new distributions of partner qualities across the season that in turn would lead to new adjustments of the choosiness strategies. We iterate this process until convergence of the sequences of choosiness strategies for males and females, such that a male or a female of any quality cannot increase their payoff by changing their choosiness strategy under the current distribution of qualities across the breeding season (i.e., when the difference in the set of strategies calculated in two successive iterations is  $< 0.001$ ). Fewer than 2,000 iterations are necessary to reach convergence.

#### Backward Iterations: Computing the Best Response Strategy of Choosiness

Because the best choice at a given time depends on future gains, which in turn depend on future choices, the best choices at each time step are calculated backward from the end of the breeding season, using dynamic programming (Houston and McNamara 1999; Roff 2010). For example, we describe briefly the backward iteration procedure for males. The final time step  $T$  is the last opportunity for reproduction, so individuals should mate with whomever they encounter and gain a payoff  $q'$ . Individuals are assumed to choose the option leading to the highest expected payoff at each time step of the season. But errors in partners' quality assessment are possible. We therefore consider a stochastic outcome of the mating decision process instead of a deterministic step function defining a clear-cut discrimination between accepted and rejected partners' qualities (McNamara et al. 1997; Dechaume-Moncharmont et al. 2016). The probability that a potential partner will be accepted is thus expressed as a sigmoid function of the difference in payoffs between accepting and rejecting the mate:

$$p_{\text{best}\delta}(q, q', t) = \frac{1 + \tanh\left\{\frac{1}{k} [w_{\text{accept}\delta}(q, q', t) - w_{\text{reject}\delta}(q, q', t)]\right\}}{2}, \quad (2)$$

where  $k$  corresponds to the slope of the sigmoid function at its inflection point (supplement 1) and specifies the

degree of error in assessing  $w_{\text{accept}_\sigma}(q, q', t) - w_{\text{reject}_\sigma}(q, q', t)$ ; (Johnstone 1997; McNamara et al. 1997). The default value of  $k$  is 0.01. Sensitivity analyses (not shown herein) revealed that considering different values for  $k$  did not change model predictions qualitatively. The expected payoff at each time step of the breeding season is defined by backward recursion from the final time step  $T$ . The expected payoff at  $t$  corresponds to the sum of the payoff acquired at  $t$  and the prospective payoff acquired from  $t + 1$  onward until the end of the season. At time  $t$ , individuals encounter a partner with a probability  $P_E(t)$ , which is calculated as follows for males and females:

$$P_{E_\sigma}(t) = \min\left(1, \frac{1}{\text{OSR}(t)}\right), \quad (3)$$

$$P_{E_\varphi}(t) = \min(1, \text{OSR}(t)).$$

The  $\text{OSR}(t)$  is the ratio between available males and available females and is calculated by the ratio of the sums of the frequencies of available individuals by quality class in each sex, noted  $f_{\text{abs}_\sigma}(q, t)$  and  $f_{\text{abs}_\varphi}(q, t)$  (eq. [4]):

$$\text{OSR}(t) = \frac{\sum_q f_{\text{abs}_\sigma}(q, t)}{\sum_q f_{\text{abs}_\varphi}(q, t)}. \quad (4)$$

Upon encountering a potential partner, individuals can then decide to accept or reject this partner depending on its quality, on its own quality, and on the distribution of available qualities. If individuals reject a partner or get rejected at a time step  $t < T$ , they nevertheless receive expected future payoffs calculated from time step  $t + 1$  (eq. [5]):

$$w_{\text{reject}_\sigma}(q, q', t) = w_\sigma(q, t + 1). \quad (5)$$

If an individual accepts a partner and gets accepted back, both of them gain an immediate payoff corresponding to the quality of their partner  $q'$ . They then have to wait until the end of their respective latency period to have another opportunity for reproduction (eq. [6]):

$$w_{\text{accept}_\sigma}(q, q', t) = q' + \sum_{i=1}^{T-t} P_{A_\sigma}(t + i) w_\sigma(q, t + i), \quad (6)$$

where  $P_{A_\sigma}(t + i) = [1 - (1/\tau_\sigma)]^{i-1} (1/\tau_\sigma)$  is the probability that a male who entered in latency period at time step  $t$  becomes newly available for reproduction at time step  $t + i$ . To calculate this probability, we assumed that the latency period ends at a constant rate. As the average duration of latency period is  $\tau_\sigma$ , at each time step  $t$ , the probability that the individual becomes newly available for reproduction during this time step is  $1/\tau_\sigma$ . The fitness for an individual of quality  $q$  at time  $t$  is therefore calcu-

lated considering all possible situations weighted by their probabilities of occurrence (eq. [7]):

$$w_\sigma(q, t) = P_{E_\sigma}(t) \sum_{q'} f_\sigma(q', t) \times [p_{\text{best}_\sigma}(q, q', t) p_{\text{resident}_\varphi}(q', q, t) w_{\text{accept}_\sigma}(q, q', t) + (1 - p_{\text{best}_\sigma}(q, q', t) p_{\text{resident}_\varphi}(q', q, t)) w_{\text{reject}_\sigma}(q, q', t)] + (1 - P_{E_\sigma}(t)) w_\sigma(q, t + 1). \quad (7)$$

The first part of the equation corresponds to the situation where individuals encounter a partner at time  $t$  (with a probability  $P_E(t)$ ). In that case, we sum the payoffs in all the possible situations weighted by their probabilities of occurrences: depending on the quality  $q'$  of the encountered partner, individuals can either mate or not. The second part of the equation corresponds to the situation where individuals do not encounter a partner at time step  $t < T$ , (with a probability  $1 - P_E(t)$ ), individuals can still expect a future payoff at the next time step. Notice that if  $t + 1 > T$ ,  $w_\sigma(q, t + 1) = 0$ .

### Costly Courtship

The previous calculations assume no direct courtship cost. It is however also possible that costly courtship may have already evolved, wherein the cost of courtship would be related to the difference in quality between potential partners (Fawcett and Johnstone 2003; Härdling and Kokko 2005), assuming, for instance, that high-quality partners attract more rivals. We here represent such cost as a simple linear cost function. When individuals of quality  $q$  choose a mate of quality  $q'$ , they now have a direct cost to pay (eq. [8]):

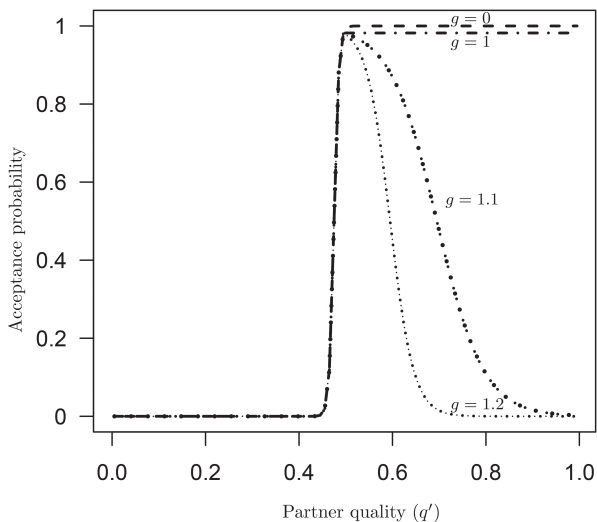
$$c(q, q') = \begin{cases} g \times (q' - q) & \text{if } q' > q, \\ 1 & \text{if } q' \leq q. \end{cases} \quad (8)$$

And their payoff is thus as follows (eq. [9]):

$$w_{\text{accept}_\sigma}(q, q', t) = q' - c(q, q') + \sum_{i=1}^{T-t} P_{A_\sigma}(t + i) w_\sigma(q, t + i). \quad (9)$$

The shape of the choosiness function (i.e., probability of acceptance as a function of partner quality) now depends on the intensity of the cost (i.e., value of  $g$ ) and goes from threshold (when  $g \leq 1$ ) to unimodal (when  $g > 1$ ), as individuals pay a cost to court a partner of better quality than themselves. The exact shape of the choosiness depends on the value of  $g$  relative to  $w_{\text{accept}}(q, q', t)$  and  $w_{\text{reject}}(q, q', t)$ , so it will vary with the chooser's quality and the time in the season (see fig. 1).





**Figure 1:** Probability to accept a partner as a function of its quality  $q'$ . The present example is calculated on the fiftieth time step of the breeding season, for different cost intensities ( $g = 0$ ,  $g = 1$ ,  $g = 1.1$ ,  $g = 1.2$ ), and the quality of the individual expressing his choosiness is  $q50$ .  $w_{\text{accept}} = q' - c(q, q')$ , (i.e., monogamy), and  $w_{\text{reject}} = 0.445$ .

### Modeling Scenarios and Measure of Choosiness

To illustrate the effect of pairing dynamics on the evolution of choosiness, we focus on a polygynandrous mating system, wherein both females and males can mate and potentially return to the mating pool after a latency period that differs between sexes ( $[\tau_{\delta} = T/4, \tau_{\varphi} = T/2]$ ). Such a dynamic mating system is common in nature and is ideal to represent potential asymmetrical fluctuations in pairing dynamics: it is indeed expected that—because they generally have a shorter latency period—males will become newly available for mating more quickly than females and will therefore be in excess in the mating market. The R code and a Shiny application, provided as online enhancements (Chevalier et al. 2020), can be used to explore the predictions for other mating systems, such as monogamy (single mating for both males and females,  $\tau_{\delta} = \tau_{\varphi} \gg T$ ) and polygyny (multiple mating for males only [ $\tau_{\delta} = T/4, \tau_{\varphi} \gg T$ ]), and for different ASR. (R code is also provided in a zip file, available online.)<sup>1</sup> We also compare noncostly ( $g = 0$ ) and costly ( $g = 1.1$ ) courtship. The optimal choosiness strategy for an individual is a set of acceptance probabilities, with one probability for every partner quality  $q'$  and time of

1. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

season  $t$ . For illustration purposes, we simplified this multidimensional metric as the inflection point of equation (2), that is, a threshold of quality (varying between  $q = 0$  and  $q = 100$ ) at which a partner will be accepted with a probability of 0.5 (fig. 1). We keep this simple metric of choosiness even when the function is unimodal (because of costly courtship). To keep things manageable, we will use discrete, representative categories of quality: high-quality (HQ,  $q = 75$ ), intermediate-quality (IQ,  $q = 50$ ), and low-quality (LQ,  $q = 25$ ) individuals.

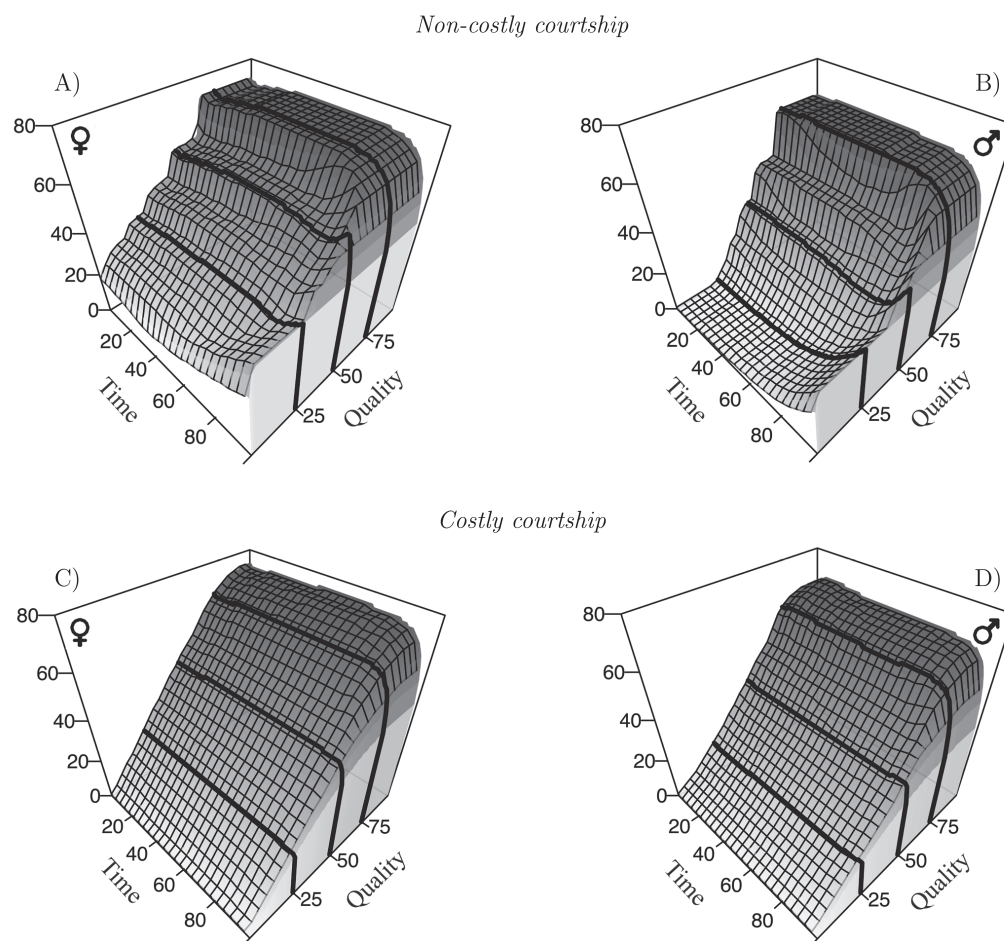
## Results

### Quality-Dependent and Flexible Optimal Choosiness

Here we first examine whether the optimal choosiness depends on the individual quality and whether this choosiness is flexible during the breeding season. In the polygynandrous mating system investigated here, with noncostly courtship, the optimal choosiness strategy is both quality dependent and flexible (fig. 2A, 2B). HQ individuals display high choosiness most of the time, but decrease it at the end of the breeding season. IQ and LQ individuals are more sensitive to the fluctuation of the mating market and decrease their choosiness when partner availability decreases. However, they take advantage of the decline in HQ individuals' choosiness to increase their choosiness near the end of the season (fig. 2A, 2B). In the present mating system, LQ males have very low choosiness, because they struggle to find females that accept them, which is demonstrated by their low probabilities to mate and to be courted and their high probability to be rejected (fig. 3). HQ individuals more easily find mates, as they are more courted and less rejected (fig. 3). It thus appears that the dynamics of mate availability generates quality dependence and flexibility of choosiness. It is consequently also influenced by the ASR and latency periods of males and females, which implies specific patterns depending on the mating system (supplement 2). For instance, in monogamy, the distribution of available partners' quality decreases continuously over time, generating a monotonous decline in choosiness and precise quality dependency (supplement 2). By contrast, in polygyny, individuals of all qualities adjust their choosiness to fluctuations in partner availability, both downward and upward, thereby displaying high flexibility (supplement 2). The Shiny application is available to visualize distribution of available partners ([https://louise64.shinyapps.io/frequency\\_available\\_individuals/](https://louise64.shinyapps.io/frequency_available_individuals/)) and optimal choosiness (<https://louise64.shinyapps.io/choosiness/>) in different mating systems (Chevalier et al. 2020).

With costly courtship, optimal choosiness varies even more continuously with the chooser's quality (i.e., increased quality dependence). But the greater the cost of

## OPTIMAL CHOOSINESS



**Figure 2:** Optimal choosiness for females and males as functions of time and individual quality, with noncostly courtship (A, B) or with costly courtship (C, D). Optimal choosiness is measured as the partner quality that an individual is ready to accept with a probability of at least 0.5. Thick black lines indicate high-quality ( $q = 75$ ), intermediate-quality ( $q = 50$ ), and low-quality ( $q = 25$ ) individuals.

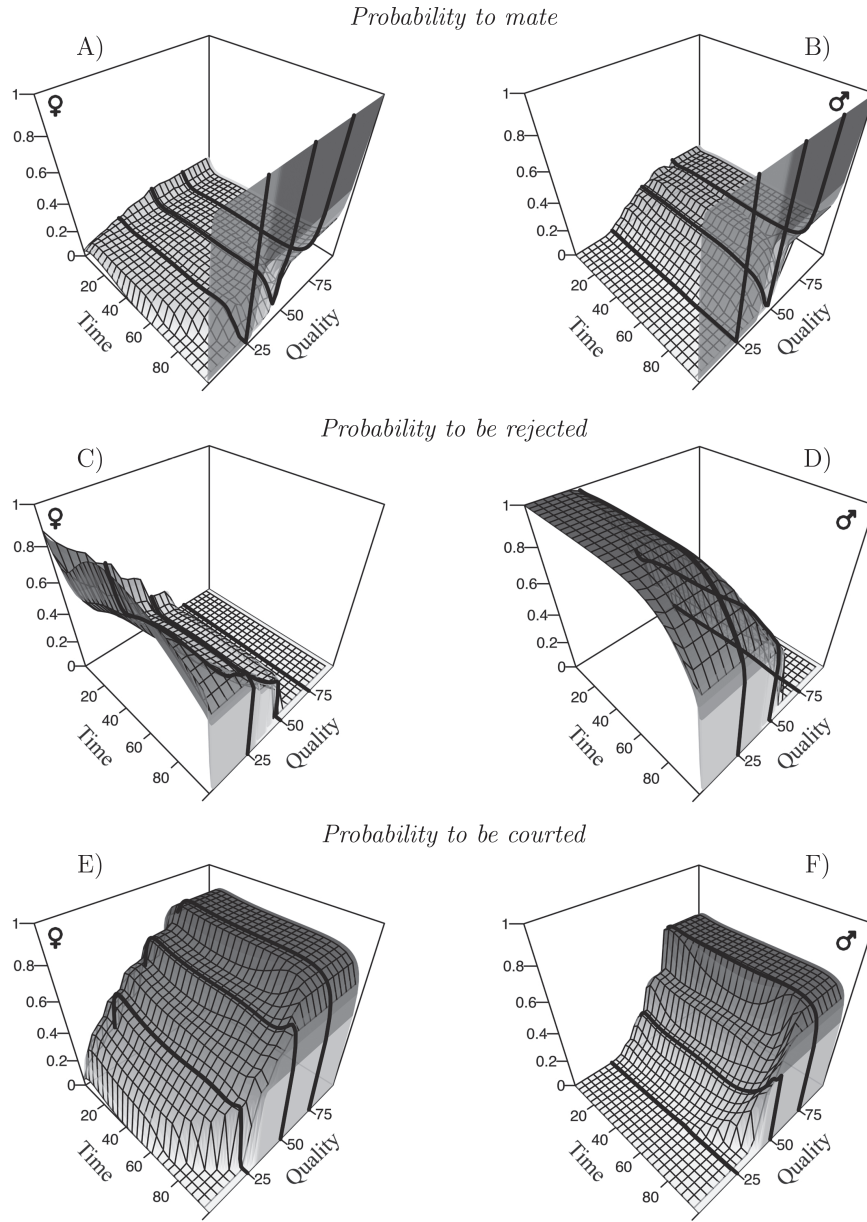
courtship, the lower the flexibility of choosiness (fig. 2C, 2D for  $g = 1.1$ ). The cost of courtship also substantially changes some behavioral aspects in the model: rejection probability even for LQ individuals (males and females) is now reduced, as they tend to select more accessible partners (fig. 2).

Changing initial distribution for individual quality  $f(q)$ —either bell shaped ( $\beta(2, 2)$ ), right skewed ( $\beta(2, 3)$ ), or uniform ( $\beta(1, 1)$ )—does not have a strong qualitative effect on the evolution of choosiness, even though, as expected, optimal choosiness decreases when the distribution of quality is biased toward LQ individuals (fig. S8; figs. S1–S8 are available online). Moreover, changing the fitness gain (initially equal to the quality of the chosen

partner) to a multiplicative gain (equal to the product of both partners' quality) does not qualitatively affect the results (fig. S7). Finally, the length of the breeding season does not qualitatively modify the choosiness either: the temporal pattern in choosiness is simply adjusted to the length of the season (data are not shown).

#### *Emerging Patterns of Interest*

As a consequence of the pairing dynamics, several observable patterns arise from the model. As expected, the unequal latency period led to differences in choosiness between sexes. Female choosiness is globally higher than



**Figure 3:** Probability to mate, be rejected, and be courted following an encounter, for females (A, C, E) and males (B, D, F). Courtship is cost free. The probability to mate is the chance an individual of quality  $q$  has to mate following an encounter (i.e., mutual choice). The probability to be rejected is the chance of being rejected by a partner that the individual would have accepted. The probability to be courted is the chance that an individual refuses a partner who would have agreed to mate. Thick black lines indicate high-quality ( $q = 75$ ), intermediate-quality ( $q = 50$ ), and low-quality ( $q = 25$ ) individuals.

male choosiness (fig. 2A, 2B). Despite this imbalance, HQ males maintain a high level of choosiness during most of the breeding season (fig. 2B). That is because the high choosiness displayed in general by females reduces the ability of less attractive males to mate with preferred females, which partially relaxes scramble competition among HQ males. It is noteworthy that the OSR, which

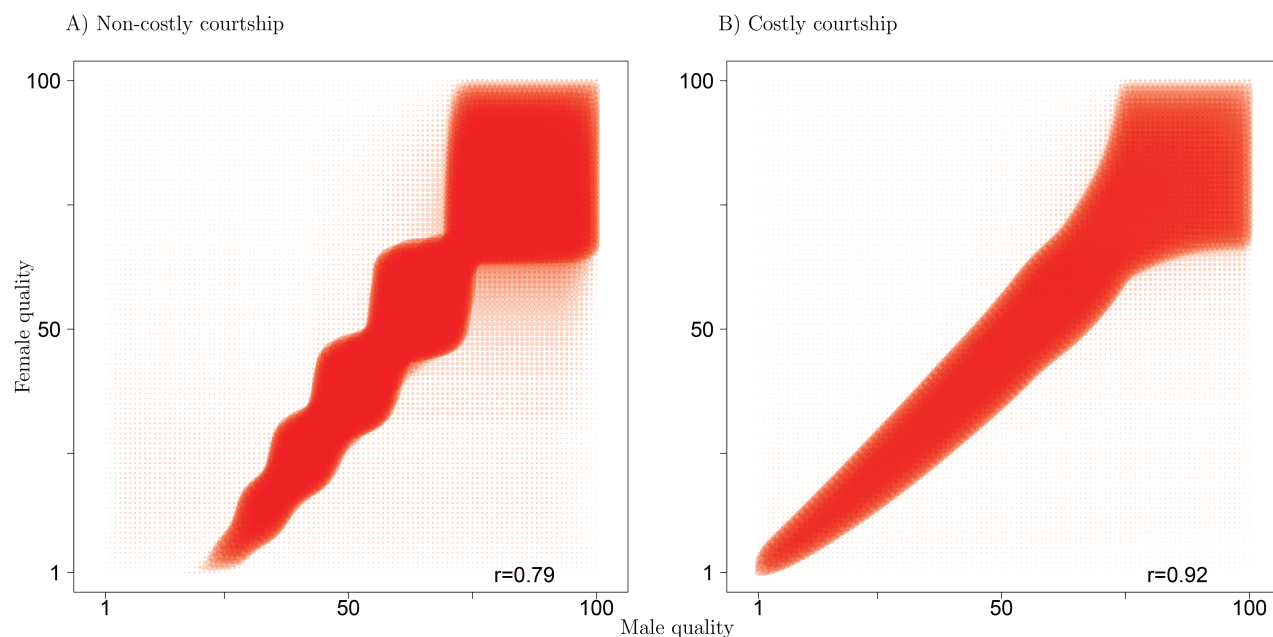
is becoming increasingly biased toward an excess of males (supplement 3), poorly describes how the competition is distributed among quality classes. Maintenance of choosiness in the HQ individuals of the common sex is also observed for other mating systems (supplement 2). Even in heavily unbalanced scenarios (extreme ASR values and very short latency periods for males), HQ males remain choosy (except

when the latency period in males is equal to 1; data not shown; R code available to explore all combinations of parameters). This makes the choosiness difference between same-sex individuals higher in males than in females (as reflected by higher variance in choosiness; supplement 3). Another significant result is that—when courtship is cost free—for both males and females, optimal choosiness is not a monotonic function of quality but instead presents some regular thresholds. For instance, females belonging to some adjacent quality classes have the same optimal choosiness (e.g., between females of quality 60 and higher; fig. 2A), meaning that these individuals compete for the same quality of mates. On some other part of the quality range, however (e.g., the quality between 50 and 60; fig. 2A), the optimal choosiness declines steeply, indicating that these females do not really compete over males of the same quality. The population (males and females) can thus be divided into subgroups of individuals competing for the same mates, such that lower-quality individuals from each competing subgroup would have a harder time finding a mate. It operates as soon as both sexes have the opportunity to have more than one mating during the breeding season (<https://louise64.shinyapps.io/choosiness/>; Chevalier et al. 2020). Interestingly, this pattern of stepped choosiness occurs despite using a fine scale for quality variation (with 100 discrete classes of quality) and is less detectable if the population is divided into fewer discrete classes of quality (such

as 10 classes; data not shown). However, as shown previously, quality dependence of choosiness increases with costly courtship by segmenting competition between individuals of close quality and thus erases this stepped choosiness pattern.

### Assortative Mating

From the pairing dynamics of the mating market, we can also predict the total frequency of mated couples between each pair of qualities during the breeding season (fig. 4). First, as expected in a polygynandrous mating system, sexual selection appears stronger in males (LQ males have negligible mating success). A general assortative mating pattern is observed in the present situation ( $r = 0.76$ ). However, its distribution with regard to female and to male quality is not linear, and we observe quality-related subgroups within which assortative mating is weaker (fig. 4A). This pattern echoes the abovementioned effect of the pairing dynamics, which splits the population into subgroups of individuals that reproduce among themselves. Interestingly, this particular motif of a quality-related subgroup of individuals mating among themselves is characteristic of the polygynandrous mating system and is relaxed when the latency period increases (supplement 4). With costly courtship, because quality dependence of choosiness is increased, these subgroups disappear and assortative mating increases substantially ( $r = 0.92$ , fig. 4B). This



**Figure 4:** Final mating pattern with noncostly courtship (A) and costly courtship (B;  $g = 1.1$ ). For a given quality of male and female, the size of the points is proportional to the frequency of pairs formed during the breeding season.



also favors the mating success of LQ males, which are now chosen by LQ females.

### Discussion

To correctly represent the pairing dynamics within the mating market, and therefore the availability of potential partners of a given sex and quality at a given time, it is essential to allow (1) choosiness to evolve in both sexes (Parker 1983; McNamara and Collins 1990; Johnstone et al. 1996; Johnstone 1997; Kokko and Monaghan 2001; Lande et al. 2001; Kokko and Johnstone 2002; Alpern and Reyniers 2005; Servedio and Lande 2006; Fawcett and Bleay 2009; Ramsey 2011; Courtiol et al. 2016), (2) realistic variation in quality within each sex (McNamara and Collins 1990; Johnstone et al. 1996; Alpern and Reyniers 2005; Ramsey 2011), and (3) potential flexibility in choosiness (Johnstone 1997; Fawcett and Johnstone 2003; Alpern and Reyniers 2005; Fawcett and Bleay 2009; Bleu et al. 2011; Ramsey 2011). Previous studies that have encompassed the three points only addressed very particular cases (i.e., monogamous balanced mating systems; Johnstone 1997; Alpern and Reyniers 2005; Ramsey 2008). By extending the integration of these three mechanisms to a wide range of mating systems, spanning a range of ASR and latency periods, we demonstrated that choosiness is likely to evolve in both sexes in most mating systems, but also to be flexible, depending on the cost of courtship. In a nutshell, our approach aims to capture the fine dynamics of the mating market, whereas previous models confined choosiness to only one sex or limited the quality variation or the extent of plasticity in choosiness.

#### *Quality-Dependent and Flexible Optimal Choosiness*

Quality dependence and flexibility in choosiness were predicted for monogamous mating systems (McNamara and Collins 1990; Johnstone 1997; Fawcett and Johnstone 2003; Alpern and Reyniers 2005; Ramsey 2011). By contrast, our model also addresses the role of ecological or physiological constraints (such as mating latency period) on the interplay between mate choice and the dynamics of the mate quality distributions, and investigates sex differences in choosiness. By allowing individuals in each quality class to fine-tune their choosiness to the variation of scramble competition experienced throughout the breeding season, we also reveal some counterintuitive strategies. Specifically, we predict an increase in choosiness for LQ and IQ individuals over the breeding season. To our knowledge, this trend has only been clearly predicted when sampling incurs a direct searching cost (Johnstone 1997)

or when individuals need to defend their mates from rivals (Fawcett and Johnstone 2003). Our model implies that when choosiness is allowed to evolve in both sexes, such an increase could in fact arise from the pairing dynamics alone without these additional costs. However, the addition of a courtship cost, which is constant throughout the breeding season and does not emerge from individual interactions (contrary to Fawcett and Johnstone 2003), will limit this flexibility. Our results also indicate that as soon as both sexes have the opportunity to mate more than once, choosiness varies noncontinuously with quality, as individuals belonging to some adjacent quality classes have the same optimal choosiness. Here, the addition of a courtship cost increases the quality dependence of choosiness.

### *Perspectives*

The fluctuating dynamics of the mating market and the associated opportunity costs are powerful drivers of the choosiness evolution in our model. Future efforts should be dedicated to bridging the gap between these fluctuations that operate on a short timescale, as we envisioned, and longer timescale models that optimize latency periods, for instance, so as to balance the contribution of both short- and long-term approaches in choosiness evolution.

### *Model Assumptions*

As in any modeling exercise, a set of assumptions underpins our analysis and findings. First, individuals are assumed to know the quality distribution of the opposite sex throughout the breeding season (within the margin of the assessment error we simulate). This depends on the presence of accurate cues and honest signals, with any sensory costs sufficiently modest to not alter the decision-making process (Shugan 1980; Wang et al. 2017). In poeciliid fish, for instance, females experiencing more variable male courtship display enhanced brain function (Wang et al. 2014; Cummings 2015), even if they may do so at a significant energetic cost. Likewise, the model calculates fitness horizons on the basis of the quality of the focal individual: this requires that each individual knows its own quality (a rather unlikely scenario; Fawcett and Bleay 2009) or that selection has generated genetic covariation in which HQ individuals are choosy and LQ individuals are less so (Servedio and Lande 2006). For a monogamous and balanced mating system, Fawcett and Bleay (2009) have explored how choosiness could evolve, on the basis of learning one's attractiveness through acceptance/rejection trials. They show that, in such conditions, variance between quality classes is increased during the first few time steps. However, when the mating market is more dynamic and less

predictable, as in most mating systems, a learning process must lag behind the fluctuations of the market, making choosiness always suboptimal (as compared with a system where individuals know their own quality). Under costly courtship, strategies become deliberately assortative, a result consistent with Fawcett and Johnstone (2003) and Härdling and Kokko (2005), where HQ individuals are better able to defend the most attractive partners. Yet costly courtship—as modeled here—does not promote flexibility. Flexibility might be favored if the cost of courtship would emerge from the interaction with rival and vary throughout the breeding season (as in Fawcett and Johnstone 2003). Still, our approach demonstrates that variance in choosiness and consequent assortative mating can be generated by the pairing dynamics alone, without needing to invoke cost constraints and interference effects. Finally, by focusing on the short-term dynamics of mate availability, we assumed constant values for variables characterizing the different mating systems, such as latency period and ASR. Other models, focusing instead on life histories and therefore on longer timescales, assume that latency period can be optimized too by considering the trade-off between mating opportunities and parental care (Kokko and Johnstone 2002; Kokko and Jennions 2003, 2008). This trade-off can affect the mating market dynamics and thus the evolution of choosiness (Kokko and Jennions 2008; Fromhage and Jennions 2016).

### *Emerging Patterns*

Evolving toward quality-dependent and flexible choosiness strategies produces distinct patterns of interest for the study of mating systems. First, choosiness should evolve frequently in both sexes, in a wide span of mating systems. Previously, many models have investigated how differences in choosiness between sex could evolve (Owens and Thompson 1994; Kokko and Monaghan 2001; Kokko and Johnstone 2002; Courtiol et al. 2016; Fromhage and Jennions 2016). In most of these results, the latency period, sex ratio at maturation, and sex-dependent breeding costs explain differences in choosiness between sexes, with the general expectation that the most common sex will be less choosy, if choosy at all. For instance, Dechaume-Moncharmont et al. (2016) showed that scramble competition suppresses choosiness in the most common sex, but they did not include the influence of other-sex choosiness on the evolution of the focal-sex choosiness. Alternatively, Courtiol et al. (2016) and Kokko and Johnstone (2002) predicted that mutual choice would mainly evolve in situations where mating latencies are very long-lasting in both sexes—thus incurring an increasing mortality probability (i.e., monogamy)—but they assumed nonflexible

choosiness. By relaxing the abovementioned assumptions, we showed that the dynamics of the mating market along the breeding season can change these expectations. As a consequence of the interplay between the choosiness of the two sexes, and of quality-dependent flexible strategies, we observed the evolution of choosiness in both sexes for a wide range of parameter spaces. Despite the fact that empirical studies addressing choosiness in both sexes remain uncommon, male choosiness has been reported even when males are the most common sex (i.e., male-biased OSR; WearingWilde 1996; Bel-Venner et al. 2008; Venner et al. 2010). Under the assumptions of the present model, optimal choosiness differs among individuals of different qualities, generating ample variance in choosiness in both sexes.

Second, whereas models investigating quality dependence in choosiness consider either only one sex (Fawcett and Johnstone 2003; Härdling and Kokko 2005; Bleu et al. 2011) or monogamous balanced mating systems (Johnstone 1997; Alpern and Reyniers 2005), our result implies that opportunity costs resulting from pairing dynamics can be a strong driver maintaining interindividual variance in choosiness within populations (which might affect the direction and strength of sexual selection (Jennions and Petrie 1997; Murphy and Gerhardt 2000)). We emphasize that interindividual variance in choosiness is not predicted to be equal between sexes (with the trivial exception of the scenario of monogamy with balanced ASR). Female variance in choosiness is indeed found to be smaller than the male variance in choosiness. Variance in choosiness has been documented in either females or males, with a possible underlying relationship to the individual quality or competitive ability (Widemo and Sæther 1999; Amundsen and Forsgren 2001; Bonduriansky 2001; Brooks and Endler 2001; Brooks 2002; Ritchie et al. 2005; Cotton et al. 2006; Bel-Venner et al. 2008; Labonne et al. 2009; Ratterman et al. 2014).

Third, there are some general relationships between mating systems and the level of quality dependence and flexibility in choosiness. In the present approach, where we focus on the intragenerational timescale, the dynamics of the mating market are highly influenced by the type of mating systems, which we here manipulated via ASR and latency period. The general picture vividly contrasts the monogamous and polygynandrous systems. In the former, remaining individuals of higher quality constantly adjust their choosiness downward to the dwindling opportunities, while LQ individuals are never choosy. The situation is far more complex in the polygynandrous and polygynous system, where flexibility is observed for individuals of all qualities, adjusting their choosiness both downward and upward, thereby sustaining variance in choosiness later in the breeding season.

Fourth, it is remarkable that in the various mating systems envisioned here, positive assortative mating always occurs (supplement 4). Its intensity (measured by the coefficient of correlation,  $r$ ) decreases with the level of unbalance in ASR and in latency periods. In unbalanced mating systems (such as polygynandry), LQ males have almost no mating success, and thus sexual selection against them is strong; but in contrast, sexual selection is relaxed among HQ individuals. Indeed, we observe a particular pattern of apparent assortment wherein the population is divided into random-mating subsets (which result from the evolution of stepped choosiness). In such case,  $r$  is not a precise indicator of assortative mating. This result is reminiscent of the results obtained by previous analytical models, which found that couples were formed between males and females belonging to the same band (interval) of quality levels in the population (McNamara and Collins 1990; Alpern and Reyniers 2005) under monogamy. Johnstone et al. (1996) also predicted similar apparent assortative mating from a nonflexible choosiness strategy throughout the breeding season. On the contrary, our predictions indicate that such clear patterns can be related to quality-dependent flexible choosiness, wherein the population is self-organized into subsets of individuals competing for the same range of partner quality. This population partition is more coarse for unbalanced mating systems, such as polygynandry, where there are a few large groups of competitors, since individuals of relatively distant quality compete (e.g., from  $q_{60}$  to  $q_{100}$ ; supplement 4). In monogamy, by contrast, the groups are much smaller and more numerous, as only individuals of very close quality are competing together (supplement 4). The fact that costly courtship might counteract this partitioning of the population is of interest for empirical observations: the shape of assortative mating plots might in fact directly hint at the existence and the extent of courtship cost in the studied population.

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### Statement of Authorship

L.C. and F.X. developed the question and research approach. L.C. developed the model structure and wrote the scripts (in R) to run simulations, conduct analyses, and visualize model output. L.C. wrote the manuscript with input from all coauthors. J.L. and M.G. contributed to defining the scope of the study, interpreting the results, and writing the manuscript. All coauthors edited and provided significant comments on the manuscript.

### Data and Code Availability

Shiny app: [https://louise64.shinyapps.io/frequency\\_available\\_individuals/](https://louise64.shinyapps.io/frequency_available_individuals/), <https://louise64.shinyapps.io/choosiness/>. GitLab: [https://gitlab.com/louiseche/mate\\_choice.git](https://gitlab.com/louiseche/mate_choice.git). These are also backed up at <https://doi.org/10.15454/JHDCQM>. Portail Data INRAE: <https://data.inrae.fr/dataset.xhtml?persistentId=doi:10.15454/JHDCQM>.

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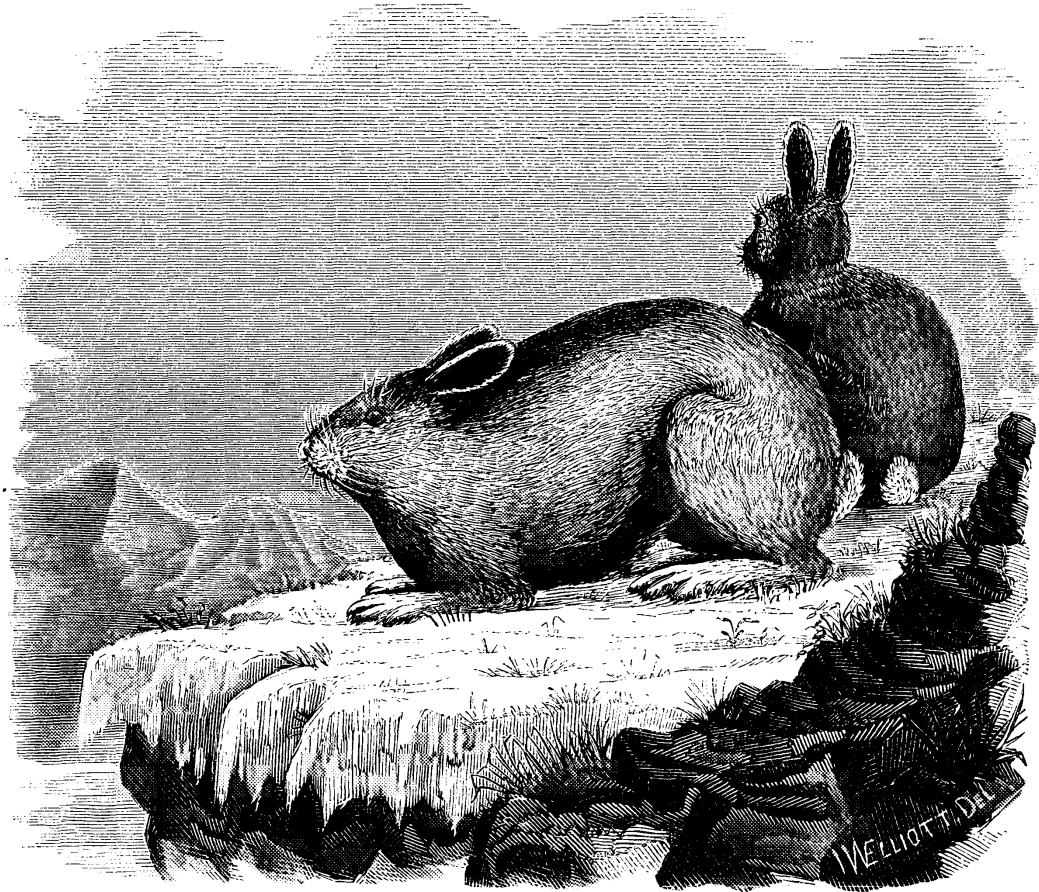
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“This interesting new species of Alpine hare, as far as our observations extend, is confined to the Wind River Mountains, where it is by no means rare, and forms a characteristic feature of the landscape, its unusually broad feet expanding with each step, forming a set of veritable snowshoes, enabling it to pass rapidly over the surface of the snow without sinking.” From “A New Species of Hare from the Summit of Wind River Mountains” by F. V. Hayden (*The American Naturalist*, 1869, 3:113–116).

# Appendix from L. Chevalier et al., “Fluctuating Dynamics of Mate Availability Promote the Evolution of Flexible Choosiness in Both Sexes”

(Am. Nat., vol. 196, no. 6, p. 000)

## Additional Methods

### Method to Calculate Quality Distribution Change throughout the Breeding Season

During the iterative calculation of the evolutionarily stable strategy, every time the best strategies are changed, one needs to update the new distributions of qualities across the breeding season  $f(q, t)_{\delta}$ , and  $f(q, t)_{\varphi}$ . We need to introduce a second notation,  $m_{\delta}(q, t)$ , as the proportion of males of quality  $q$  available among the males of this quality at time step  $t$ , and  $m_{\varphi}(q, t)$  as the proportion of females of quality  $q$  available among the females of this quality at time step  $t$ . Initially, all individuals are unmated, so that  $m_{\delta}(q, 1) = m_{\varphi}(q, 1) = 1$  and  $f_{\delta}(q, 1) = f_{\varphi}(q, 1) = f(q)/\sum_q f(q)$ . We express the relative frequency of males and females  $f(q, t)_{\delta}$ , and  $f(q, t)_{\varphi}$  as a function of  $m(q, t)_{\delta}$ , and  $m(q, t)_{\varphi}$ :

$$\begin{aligned} f_{\delta}(q, t) &= \frac{m_{\delta}(q, t)f_{\delta}(q, 1)}{\sum_q m_{\delta}(q, t)f_{\delta}(q, 1)}, \\ f_{\varphi}(q, t) &= \frac{m_{\varphi}(q, t)f_{\varphi}(q, 1)}{\sum_q m_{\varphi}(q, t)f_{\varphi}(q, 1)}. \end{aligned} \tag{A1}$$

In equation (A1),  $m_{\delta}(q, t)f_{\delta}(q, 1)$  gives the proportion of males of quality  $q$  available at time step  $t$  among all the males, and  $\sum_q m_{\delta}(q, t)f_{\delta}(q, 1)$  gives the proportion of male (all qualities combined) available among all the males. The proportion of individuals available of each quality  $q$  is recursively calculated as follows:

$$\begin{aligned} m_{\delta}(q, t+1) &= m_{\delta}(q, t) \left[ 1 - P_{E_{\delta}}(t) \sum_{q'} f_{\varphi}(q', 1) p_{\text{new}_{\delta}}(q, q', t) p_{\text{new}_{\varphi}}(q', q, t) \right] \\ &\quad + [1 - m_{\delta}(q, t)] \times \frac{1}{\tau_{\delta}}, \\ m_{\varphi}(q, t+1) &= m_{\varphi}(q, t) \left[ 1 - P_{E_{\varphi}}(t) \sum_{q'} f_{\delta}(q', 1) p_{\text{new}_{\varphi}}(q, q', t) p_{\text{new}_{\delta}}(q', q, t) \right] \\ &\quad + [1 - m_{\varphi}(q, t)] \times \frac{1}{\tau_{\varphi}}. \end{aligned} \tag{A2}$$

In equation (A2), the proportion of individuals of quality  $q$  available at  $t+1$ ,  $m_{\delta}(q, t+1)$ , is computed from the probability of individuals to encounter a partner ( $P_{E_{\delta}}(t)$  for males and  $P_{E_{\varphi}}(t)$  for females) and to mate with an encountered partner, plus the probability that individuals in refractory period becomes available.

**Table A1:** Symbol table

Symbol	Definition	Default value
$f_{\delta}(q, q', t)$	Frequency of males of quality $q$ among all males available (all quality combined) at time $t$	Variable
$m_{\delta}(q, t)$	Proportion of males of quality $q$ available among all males of quality $q$ (i.e., available males plus mated males)	Variable
$P_{\text{resident}\delta(\varphi)}(q, q', t)$	Choosiness strategy for males (respectively females) of quality $q$ , which is a matrix of acceptances probabilities for every possible partner's quality $q'$ and at each time step	Variable
$P_{\text{best}\delta(\varphi)}(q, q', t)$	"Best response" choosiness strategy for males that yields the maximum payoff in a population of competitors and mates using "resident" strategy	Variable
$P_{\text{new}\delta(\varphi)}(q, q', t)$	New resident strategy calculated with the resident choosiness strategy of the previous iteration and the best response choosiness for this resident strategy	Variable
$\lambda$	Damping term in the iterative calculation of the optimal strategy	.1
$P_{E\delta}(t)$	Probability a male encounter a partner at time $t$	Variable
$w_{\text{accept}\delta}(q, q', t)$	Expected payoff for a male of quality $q$ if he mates with a partner of quality $q'$ at time $t$	Variable
$w_{\text{reject}\delta}(q, q', t)$	Expected payoff for a male of quality $q$ if he rejects the mating with a partner of quality $q'$ at time $t$	Variable
$w_{\text{reject}\delta}(q, t)$	Expected fitness for a male of quality $q$ at time $t$	Variable
$c(q, q')$	Cost of courtship	Variable
$g$	Parameter tuning the intensity of courtship cost	1.1
OSR	Operational sex ratio (ratio of available males over available females at time step $t$ )	Variable
ASR	Adult sex ratio (ratio of available males over available females at the beginning of the breeding season)	1
$T$	Length of the breeding season	100
$\tau_{\delta}$	Mean time out for males	$\frac{1}{4}T$ or $T$
$\tau_{\varphi}$	Mean time out for females	$\frac{1}{2}T$ or $T$
$Q$	Number of quality classes	100
$k$	Degree of error when making choice	.01

Online Supplement:

Fluctuating dynamics of mate availability promote the  
evolution of flexible choosiness in both sexes,  
*The American Naturalist*

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*Supplementary 1: Acceptance and the effect of  $k$  (degree of error)*

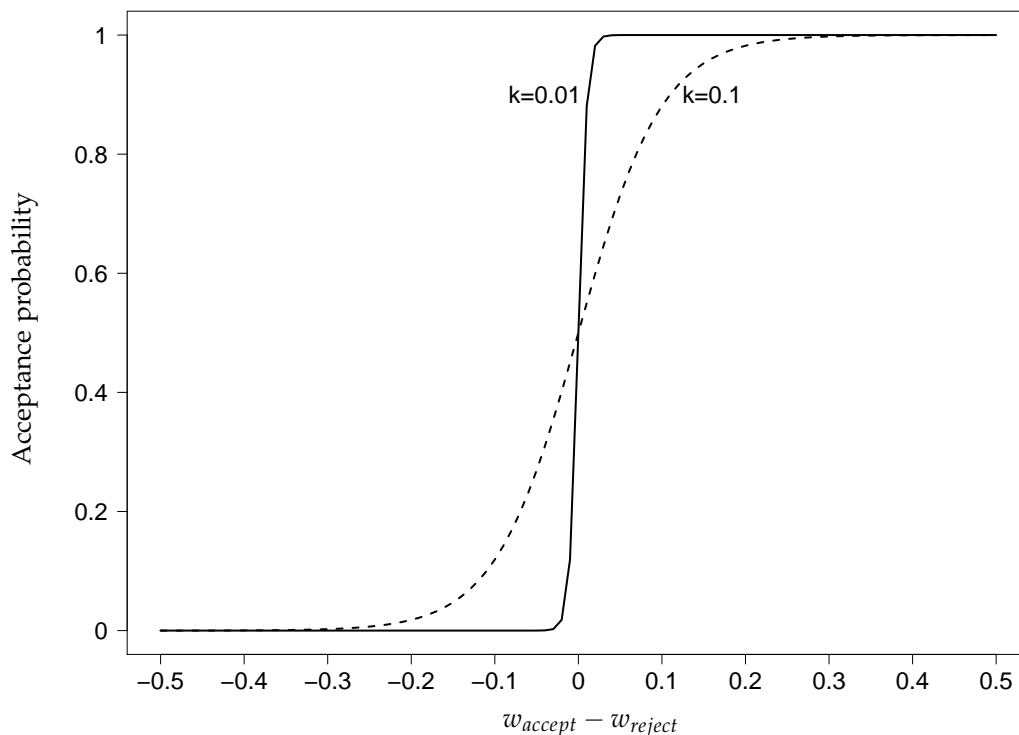


Figure S1: Probability that a potential partner will be accepted, as a function of the difference in payoffs between accepting and rejecting a mate, for two different values of  $k$ . Lower value of  $k$  indicates lower level of error.

## Supplementary 2: Optimal choosiness and partners availability in others mating systems

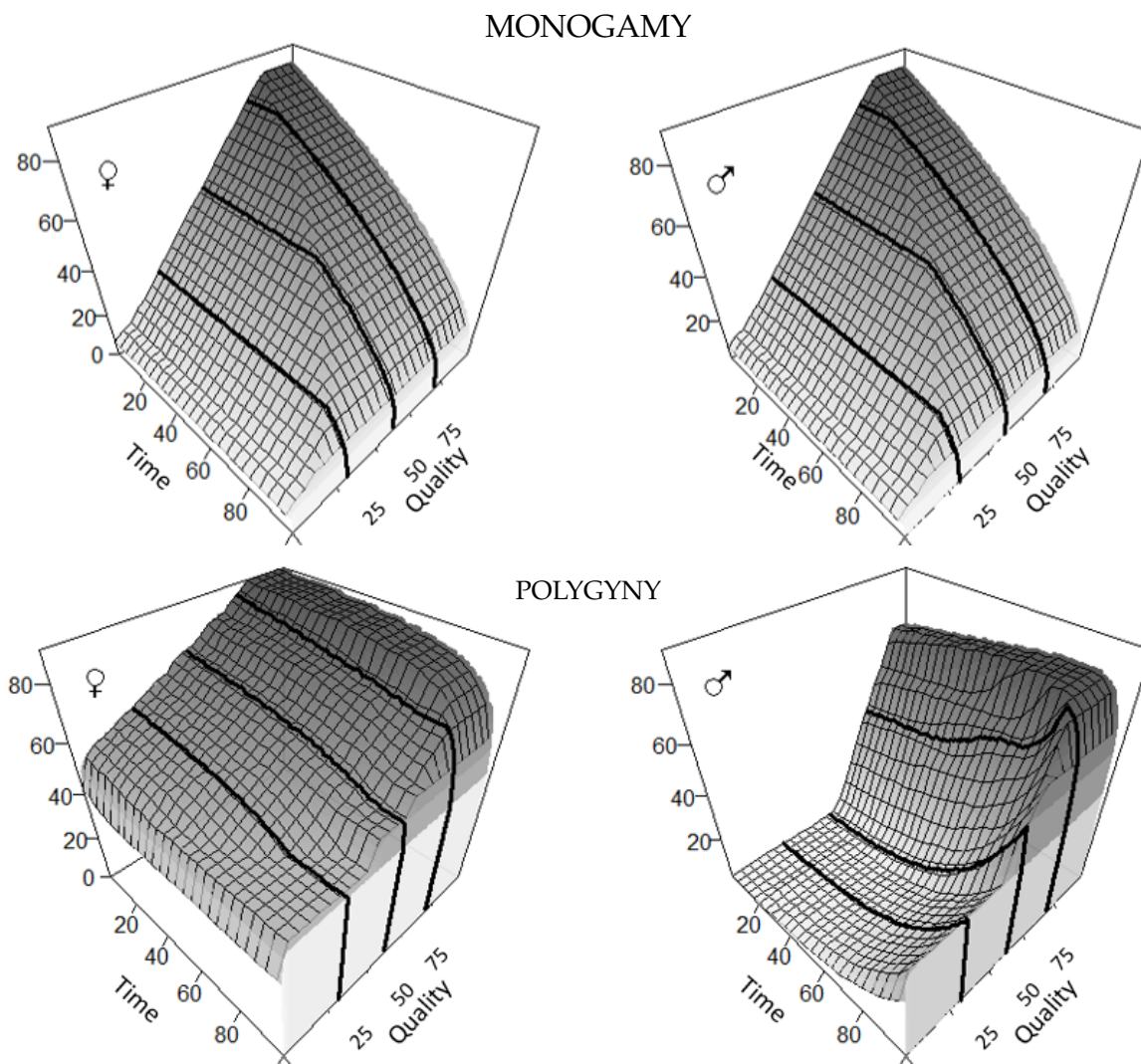


Figure S2: Optimal choosiness for females and males as functions of time and individual quality, for monogamy ( $\tau_{\sigma} = \tau_{\phi} \gg T$ ) and polygyny ( $\tau_{\sigma} = \frac{\tau}{4}, \tau_{\phi} \gg T$ ). Optimal choosiness is measured as the partner quality that an individual is ready to accept with at least a probability of 0.5. Thick black lines indicates High Quality (HQ,  $q = 75$ ), Intermediate Quality (IQ,  $q = 50$ ) and Low Quality (LQ,  $q = 25$ ) individuals.

Supplement to Chevalier et al., "Evolution of flexible choosiness," *Am. Nat.*

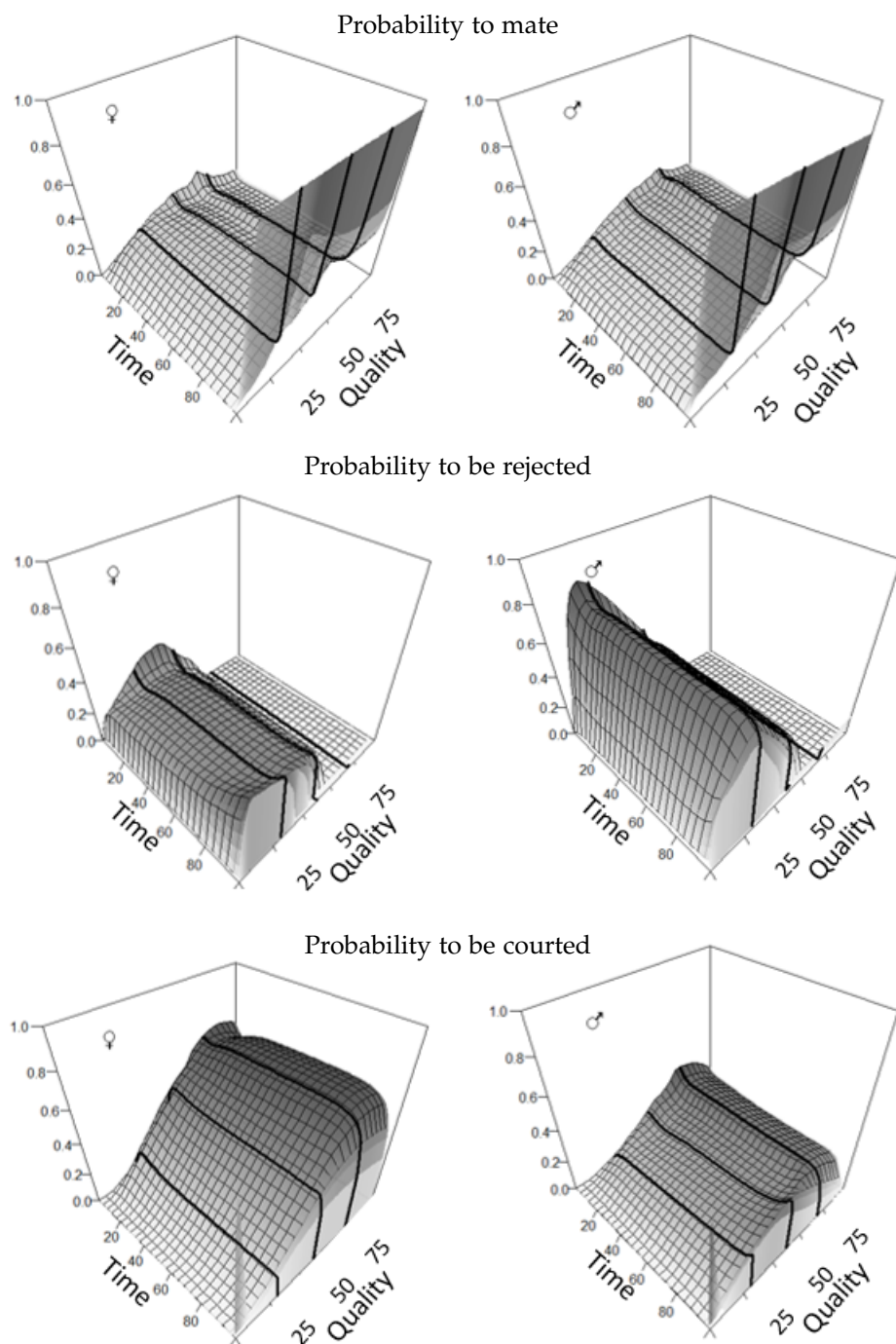


Figure S3: The probability to mate, to be rejected, and to be courted following an encounter, for females (left panels) and males (right panels). Courtship is costly ( $g = 1$ ). The probability to mate is the chance an individual of quality  $q$  has to mate following an encounter (i.e. mutual choice). The probability to be rejected is the chance of being rejected by a partner that the individual would have accepted. The probability to be courted is the chance that an individual refuses a partner who would have agreed to mate. Thick black lines indicates High Quality (HQ,  $q = 75$ ), Intermediate Quality (IQ,  $q = 50$ ) and Low Quality (LQ,  $q = 25$ ) individuals.

Supplement to Chevalier et al., "Evolution of flexible choosiness," *Am. Nat.*

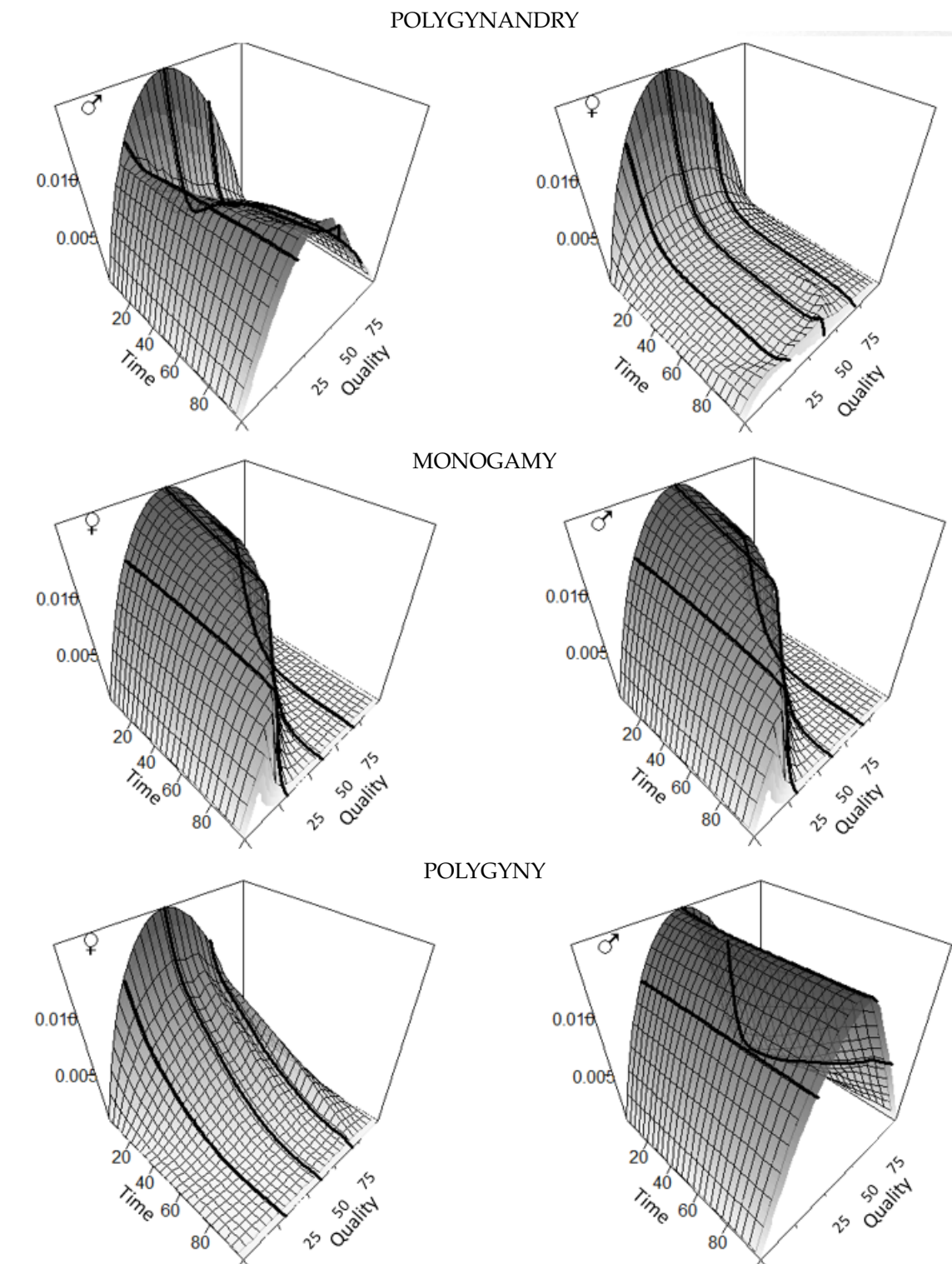


Figure S4: Distribution of partners availability as a function of their quality and time, for polygynandry, monogamy and polygyny. Availability is calculated as the absolute frequency of remaining individuals. Thick black lines indicate High Quality (HQ,  $q = 75$ ), Intermediate Quality (IQ,  $q = 50$ ) and Low Quality (LQ,  $q = 25$ ) individuals.



### Supplementary 3: Choosiness variance in different mating systems

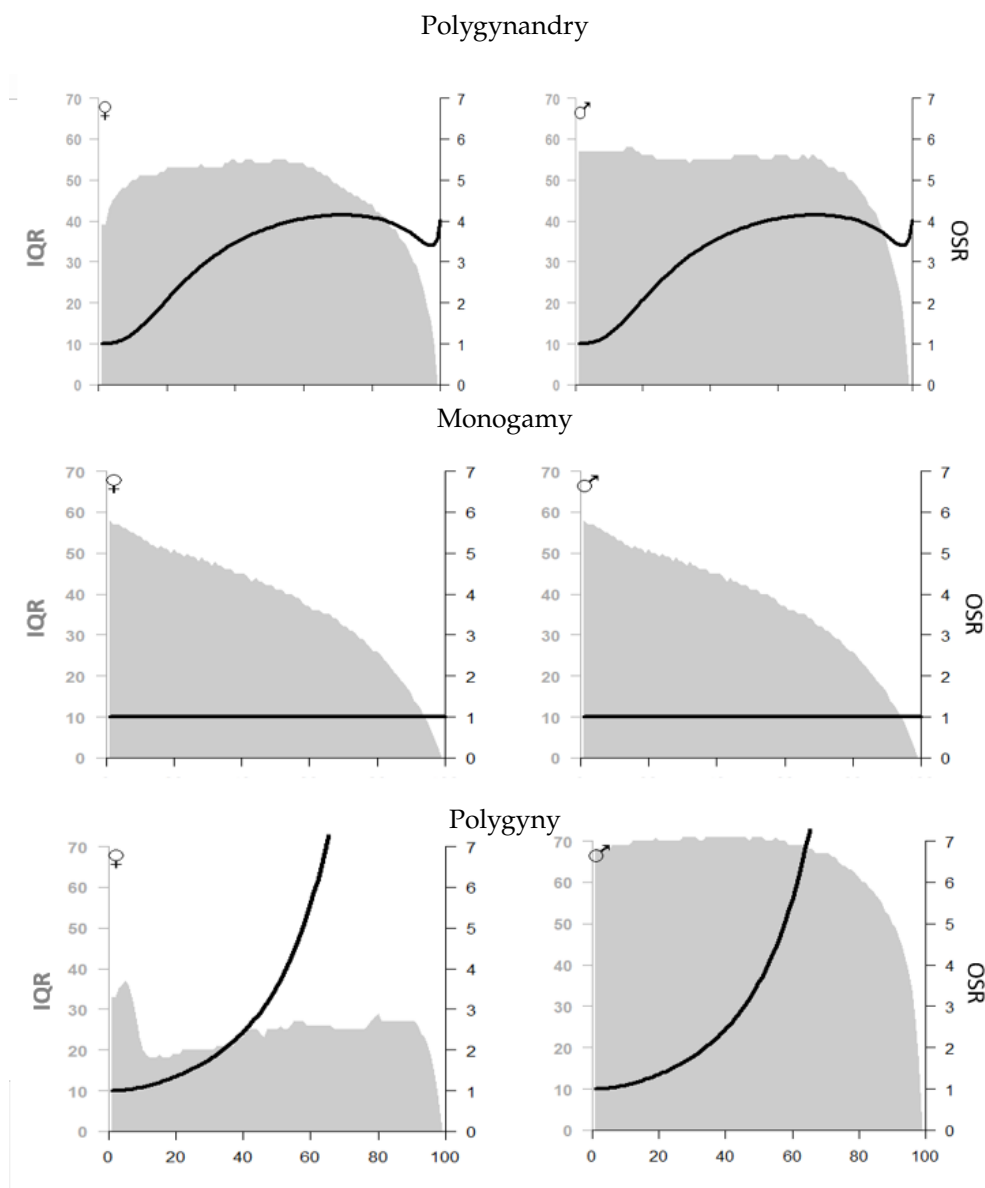


Figure S5: Variance in optimal choosiness measured as the interquartile range (IQR) and OSR (thick black line) along the breeding season for different mating systems with  $ASR = 1$ . Monogamy:  $\tau_{\sigma} \gg T$ ,  $\tau_{\phi} \gg T$ , Polygyny:  $\tau_{\sigma} = \frac{1}{2}T$ ,  $\tau_{\phi} \gg T$ . Variance in choosiness is calculated as the interquartile range. OSR is the proportion of males to females (all qualities combined).

### Supplementary 4 : Assortative mating in different mating systems

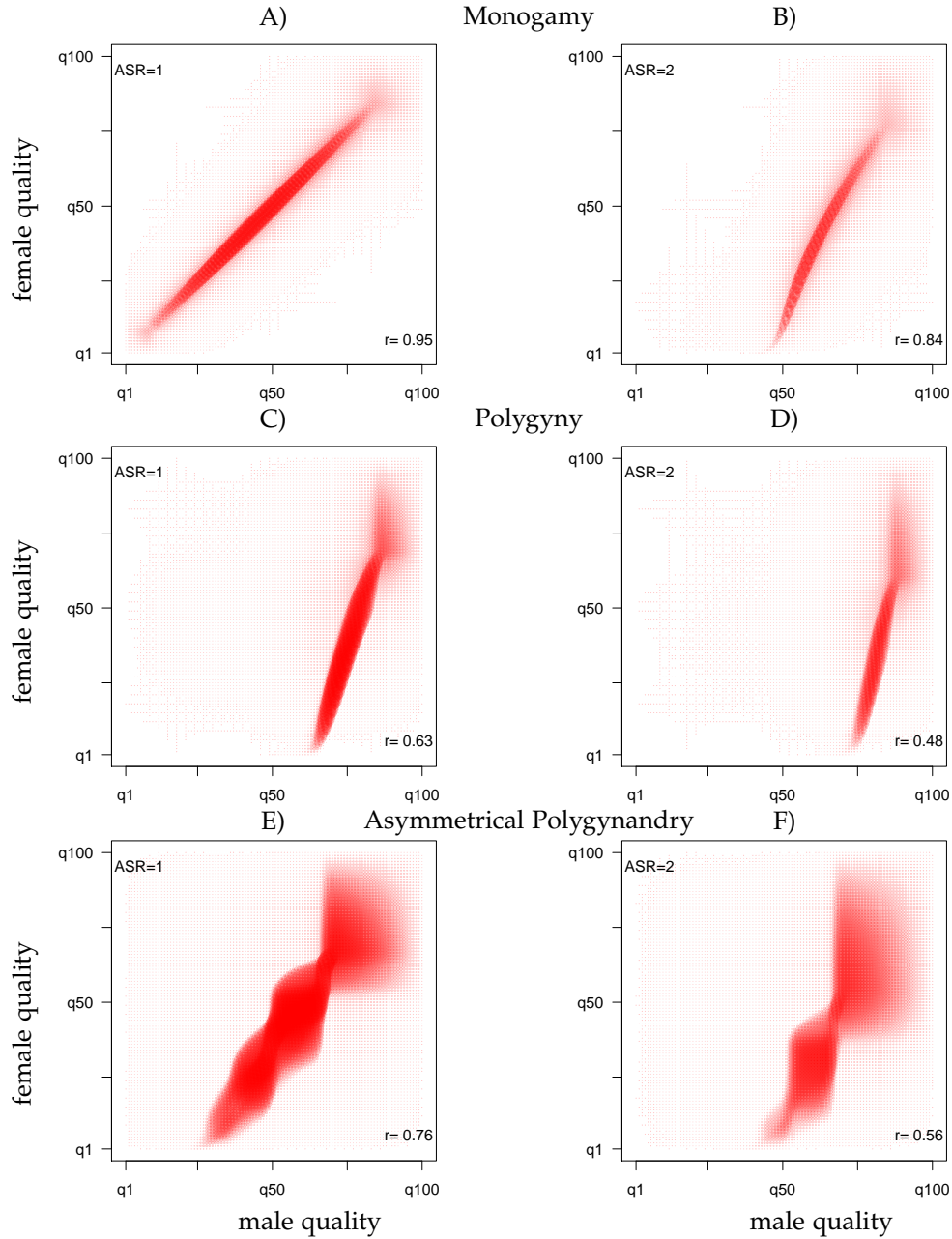


Figure S6: Final mating patterns for different mating systems with  $ASR = 1$  and  $ASR = 2$ . Monogamy:  $\tau_{\sigma} \gg T$ ,  $\tau_{\phi} \gg T$ , Polygyny:  $\tau_{\sigma} = \frac{1}{2}T$ ,  $\tau_{\phi} \gg T$ , Asymmetrical polygynandry:  $\tau_{\sigma} = \frac{1}{4}T$ ,  $\tau_{\phi} = \frac{1}{2}T$ . The size of the points is proportional to the frequency of pairs formed between each quality during the breeding season.

## Supplementary 5 : Sensitivity of the results

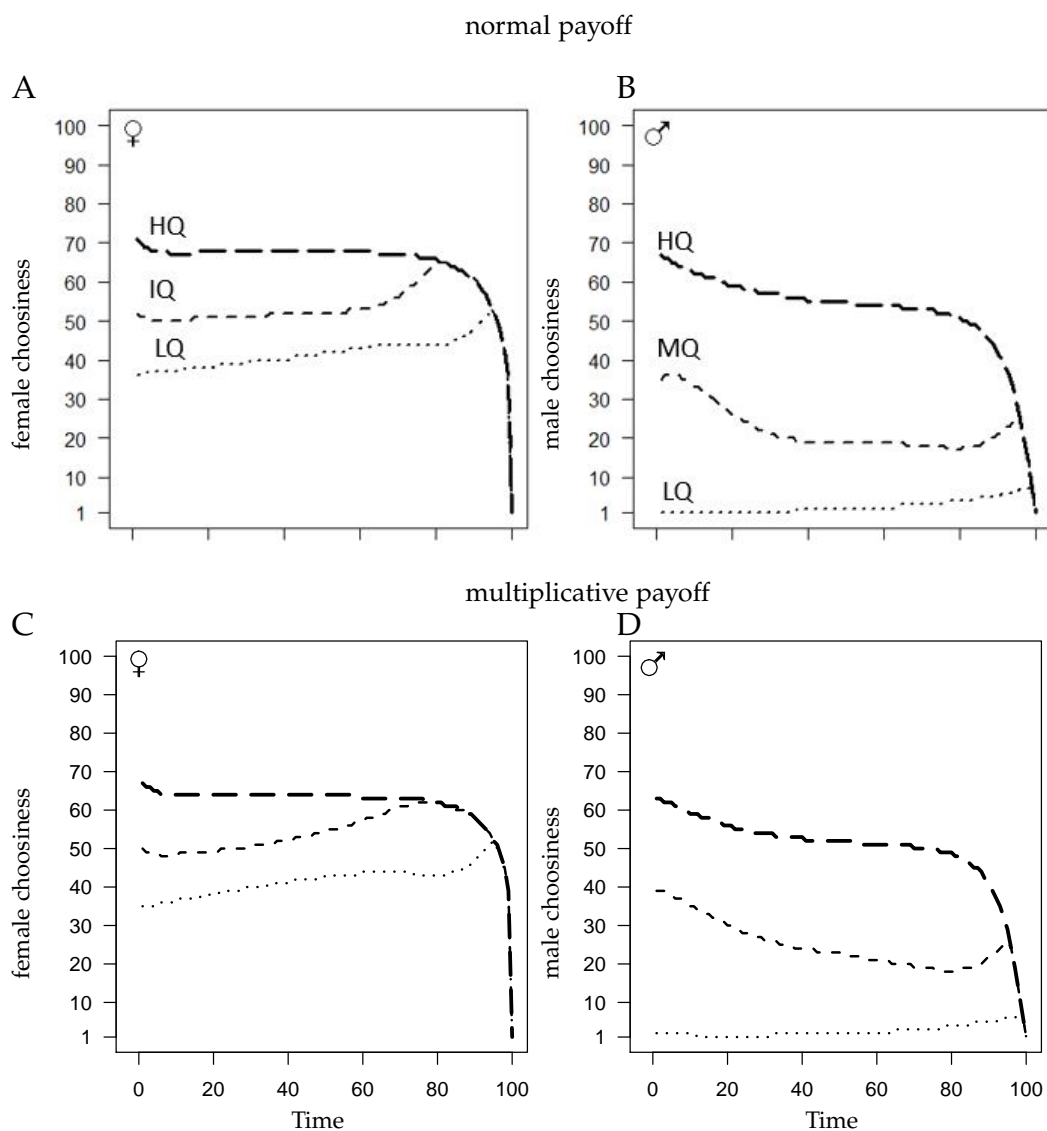


Figure S7: Effect of payoff on the optimal choosiness in a polygynandrous mating system ( $\tau_{\sigma^*} = \frac{1}{4}\tau$ ,  $\tau_{\varphi} = \frac{1}{2}T$ ). The optimal choosiness is plotted for three classes of qualities, high-quality (HQ) correspond to individuals of quality  $q_{75}$ , intermediate-quality (IQ) correspond to individuals of quality  $q_{50}$ , low-quality (LQ), correspond to individuals of quality  $q_{25}$ . A, B, the payoff is the quality of the mating partner, C, D, the payoff is the product of qualities.

Supplement to Chevalier et al., "Evolution of flexible choosiness," *Am. Nat.*

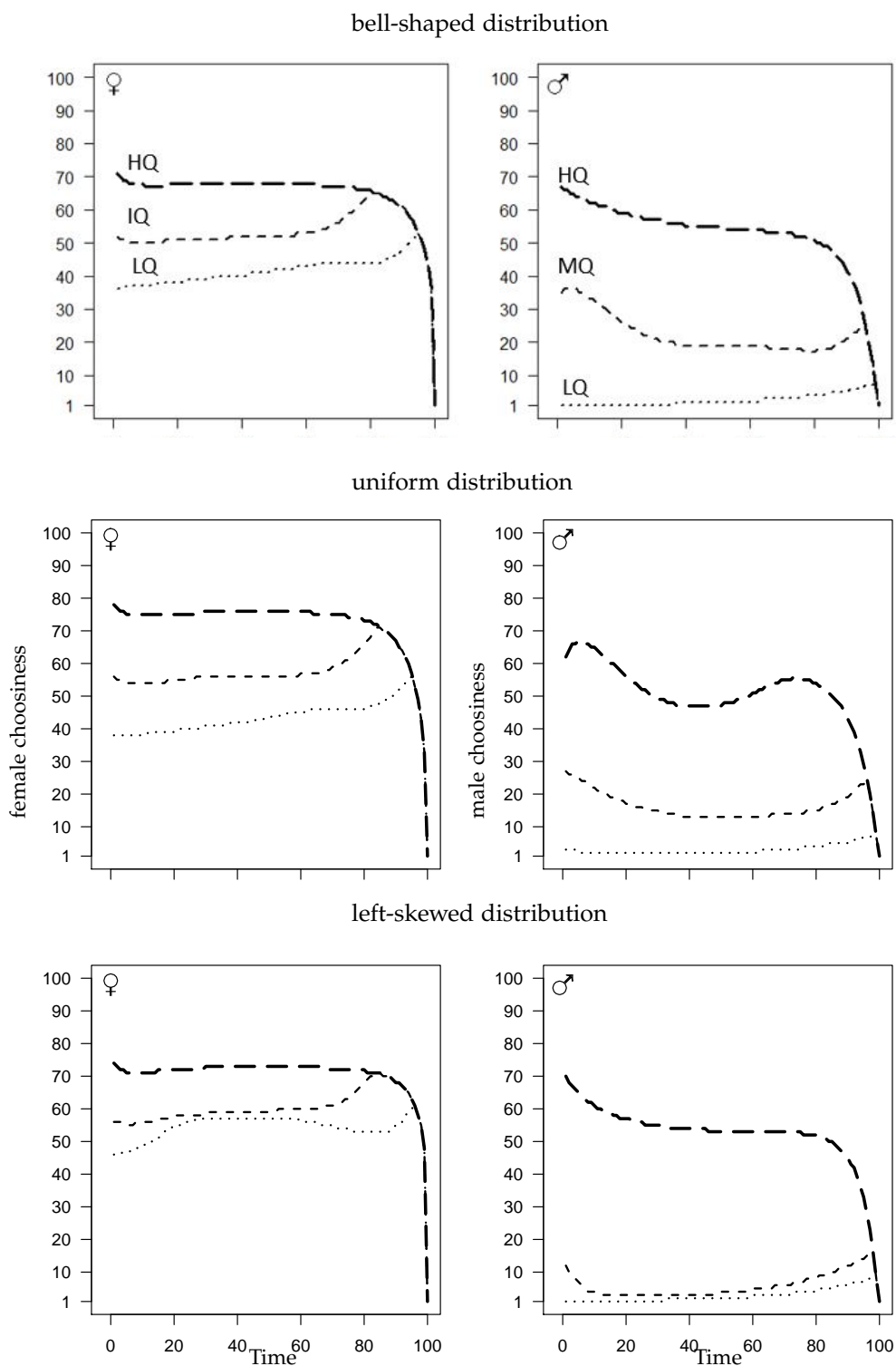


Figure S8: Optimal choosiness of males and females for different initial distributions of individual's quality. Bell-shaped distribution ( $\beta(2,2)$ ), uniform distribution ( $\beta(1,1)$ ) and left-skewed distribution ( $\beta(3,2)$ )