

Within-population variation in female mating preference affects the opportunity for sexual selection and the evolution of male traits, but things are not as simple as expected

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Abstract

Females from the same population usually have phenotypic variation in their mating preferences. However, the effects of this within-population variation on the sexual selection acting on males are still unclear. We used individual-based models to explore how within-population variation in female preference (i.e. which male trait value is preferred) and preference strength (i.e. how strong the preference is) affects the opportunity for sexual selection (I_s) and the evolution of a sexually selected male trait. We found the highest I_s values when females had high variation in preference and an open-ended preference function. The lowest I_s occurred when the magnitude of variation in female preference and male trait value were the same and preference function was closed. Male trait exaggeration was higher when there was high within-population variation in preference and females had an open-ended preference function. Also, higher male trait variation was maintained by high variation in preference, but only for a closed preference function. Thus, we found that only within-population variation in female preference, not in preference strength, influences the opportunity for sexual selection and the evolution of sexually selected male traits. Moreover, we found that the shape of the preference function (i.e. open-ended or closed) and the magnitude of within-population variation in female preference compared to male trait variation also influences the I_s and consequently the evolution of male traits.

KEYWORDS

disruptive selection, individual-based model, male trait exaggeration, mate choice, preference function, preference strength, sexual selection

1 | INTRODUCTION

A widespread assumption of sexual selection studies is that females from the same population are consistent in their preferences for particular male traits, that is, within-population variation in female mating preferences is negligible or nonexistent (reviewed by Cézilly, 2015; Widemo & Sæther, 1999). However, there is growing evidence that females from the same population can have high

phenotypic variation in their mating preferences (e.g. Kelly, 2018; Neelon, Rodríguez, & Höbel, 2019; Rodríguez, Hallett, Kilmer, & Fowler-Finn, 2013; see also Table S1 of Appendix S1). At least for some species, this variation is determined mainly by genetic variation (reviewed by Bakker & Pomiankowski, 1995; Jennions & Petrie, 1997; Kelly, 2018; see also Brooks & Endler, 2001; Rodríguez, Hallett, et al., 2013; Sharma, Tregenza, & Hosken, 2010). For many other species, in turn, variation in female mating preferences is

determined by the interaction between genes and environmental conditions (reviewed by Narraway, Hunt, Wedell, & Hosken, 2010), such as temperature (e.g. Ingleby, Hunt, & Hosken, 2010), females' social experience before adulthood (e.g. Macario, Croft, Endler, & Dardena, 2017; Madden & Whiteside, 2013), food availability (e.g. Griggio & Hoi, 2010; Hernandez-Jimenez & Rios-Cardenas, 2017; Hunt, Brooks, & Jennions, 2005) and parasite load (e.g. Dakin & Montgomerie, 2014). To better understand the consequences of female mating preferences on the sexual selection acting on males and on the evolution of sexually selected male traits, we need theoretical models that include within-population variation in female mating preferences. In what follows, we first define the basic terminology currently used to describe mating preferences. Then, we comment potential implications of variation in mating preferences for the opportunity for sexual selection and the evolution of sexually selected male traits. Although many ideas discussed below apply to both pre- and post-copulatory mate choice, our focus here is only on precopulatory mate choice.

Mating preference is formally defined as the female's propensity to mate with males with particular phenotypes (Jennions & Petrie, 1997), and it is commonly described by a preference function (Lande, 1981) that relates the mating probability (y -axis) to a trait expressed by the males (x -axis). Preference functions have at least two components that may vary independently from each other: (a) the *preference*, which is the trait value preferred by a female, and (b) the *preference strength* which is how strongly a female will reject males with trait values different from her preference (Kilmer et al., 2017). Thus, within-population variation in female preference functions

includes interindividual variation in preference, preference strength or both (empirical examples in Table S1; see also Figure 1).

There are many possible shapes of preference functions (theoretical examples in Edward, 2014; Kilmer et al., 2017; Wagner, 1998), but we highlight two of them, which are perhaps the most commonly reported in the empirical literature on mate choice (see examples in Gerhardt, 1991; Ritchie, 1996; Rodríguez, Hallett, et al., 2013). The first shape is the 'sigmoid', which is an example of open-ended preference function according to which females of a given population or species prefer males with extreme trait values (see example in Figure 1a–c). In this case, females of the same population can vary in the value of their preference, the preference strength or both (Figure 1b,c, respectively). Within-population variation in preference and/or preference strength of females showing an open-ended preference function has been reported for some species in both laboratory and field studies (e.g. Lynch, Crews, Ryan, & Wilczynski, 2006; Lyons, Beaulieu, & Sockman, 2014). The second shape is the 'bell-shaped', which is an example of closed preference function, according to which females of a given population or species prefer males with intermediate trait values (Figure 1d–f). In this case, females of the same population can also vary in the value of their preference, preference strength or both (Figure 1d,e). Closed preference functions have been reported for some traits of male acoustic call as well as for species with assortative mating. In some of these species, females show within-population variation in preference, preference strength and even in the shape of the preference function (e.g. McGuigan, Van Homrigh, & Blows, 2008; Neelon et al., 2019; Ritchie, 1996; Rodríguez, Hallett, et al., 2013).

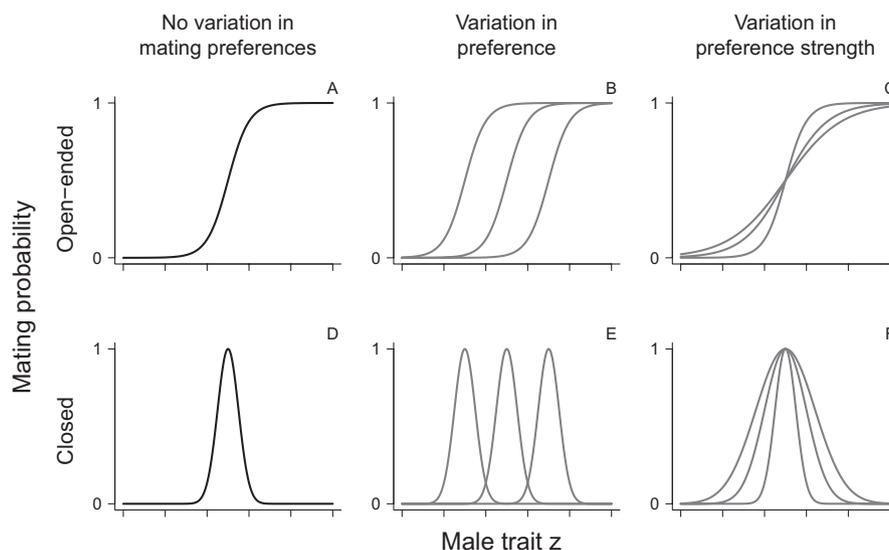


FIGURE 1 Open-ended and closed preference functions describing the probabilities of a female mating with a male showing a sexually selected trait value z . In panels (a) and (d), there is no within-population variation in female preference function (control simulations); thus, all females of the population are described as a single line. The remaining panels show (b) within-population variation for females with open-ended preferences varying in their preference, represented by the dispersion of individual lines along the x -axis and (e) closed preference functions with females from the same population varying in their preferences, represented by individual lines with different peaks. For both shapes of preference function, within-population variation in preference strength is represented by lines with different slopes (panels c and f, respectively)

Within-population variation in female mating preferences may have several consequences for sexual selection because the mating probability of a male is not determined by his attractiveness to all females of the population, but instead by his attractiveness to individual females (Brooks & Endler, 2001). Thus, a male that is not preferred to most females in a population but is highly preferred by few females may have an equal or even higher mating success than a male that is moderately preferred to all females (Jennions & Petrie, 1997). As a result, variation in female mating preferences is expected to decrease variation in male mating success and consequently to reduce the opportunity for sexual selection on males (e.g. Brooks & Endler, 2001; Cotton, Rogers, Small, Pomiankowski, & Fowler, 2006;

Ingleby et al., 2010). Thus, within-population variation in female mating preferences may also have major consequences for the evolution of sexually selected male traits. For instance, sustained directional or stabilizing sexual selection arising from female preferences is expected to reduce genetic variability in sexually selected male traits (Rowe & Houle, 1996; but see Homrigh, Higgie, McGuigan, & Blows, 2007). However, if females from the same population show variation in mating preferences, because they vary in preference and/or preference strength, it is expected that higher variability in male traits is maintained over time (Day, 2000; Jennions & Petrie, 1997; Widemo & Sæther, 1999; see also Rodríguez, Boughman, et al., 2013 for an example of among-population variation in female mating

TABLE 1 List of symbols used in the text. Individual descriptors are values that vary among individuals within each population and determine individual viability and mating probabilities. Output variables are the population-level variables we measured at the end of the mating season (in the short-term simulations) or after 50 generations (in the long-term simulations). Finally, model parameters are input variables. Their values are fixed within each simulation replicate but vary among different scenarios

Symbol	Description	Values/distribution
Individual descriptors and probabilities		
z	Male trait under sexual selection	In the short-term simulations and first generation of the long-term simulations: truncated Gaussian distribution with mean φ , standard deviation σ_z and minimum zero In the long-term simulations, determined by Equation 4
p	Individual female preference	Truncated Gaussian distribution with mean p_{mean} , standard deviation σ_p and minimum zero
s	Female preference strength	Truncated Gaussian distribution with mean s_{mean} , standard deviation σ_s and minimum zero
P_{ij}	Probability of copulation between female i and male j	Given by Equation 1 (open-ended preference function) or Equation 2 (closed preference function)
V_j	Viability (probability of survival) of a male j	Given by Equation 4
ε	Difference between offspring z and the mean z of its parent's values	Normal distribution with mean zero and standard deviation r
Output variables		
z_{mean}	Mean of male trait z	–
z_{SD}	Standard deviation of male trait z	–
I_s	Opportunity for sexual selection	Given by Equation 3
g	Hedge's g (absolute standardized difference between scenarios)	–
Model parameters		
N	Population size	2,000
σ_z	Initial standard deviation of male trait z (initial value in the long-term simulations)	1
p_{mean}	Mean female preference p	5
σ_p	Standard variation in female preference p	0, 0.25, 0.5, 1.0 and 2.0
s_{mean}	Mean female preference strength s	2
σ_s	Standard deviation in female preference p	0, 0.1, 0.2, 0.4 and 0.8
φ	Optimal value of male trait z under stabilizing natural selection, and also the initial mean value of male trait z in the long-term simulations	5
γ	Intensity of natural selection acting on male trait z in the long-term simulations	0.05 and 0.2
r	Standard deviation of ε (represents the square root of the segregation variance of male trait z)	0.2

preferences). Moreover, it has also been proposed that within-population variation in female preferences decreases or even prevents exaggeration of sexually selected male traits over time due to variation in the strength and direction of sexual selection (Mead & Arnold, 2004).

Although the verbal predictions presented above may sound intuitive, to our knowledge, there is no formal theoretical investigation about the effects of within-population variation in female preference and preference strength on the sexual selection acting on male traits. We do not know how much variation in these components of the female preference functions is necessary to influence the opportunity for sexual selection (*sensu* Lande and Arnold 1983) and, ultimately, male trait evolution. Moreover, we do not know whether the effects of variation in female preferences differ depending on the shape of the preference function (e.g. open-ended and closed functions). In this study, we used individual-based models to fill these gaps and provide formal theoretical predictions on how variation in female preference and preference strength influences the opportunity for sexual selection and the evolution of sexually selected male traits.

2 | MATERIALS AND METHODS

2.1 | General approach

We used individual-based models (IBMs) to simulate populations in which females have preference for a certain sexually selected male trait (e.g. an ornament, an advertising call or a courtship display), and there is within-population variation in one of the components of the females' preference function, that is preference or preference strength. IBMs are a class of computational models used for simulating and exploring short- and/or long-term effects of the actions and interactions between individuals and their traits. The use of IBMs allows the simulation of complex ecological and evolutionary scenarios, which otherwise would be hard or impossible to do using analytical approaches (Grimm & Railsback, 2005; Kuijper, Pen, & Weissing, 2012). In our study, we explore the effects of within-population variation in female mating preferences on (a) the opportunity for sexual selection acting on males (i.e. a short-term effect) and (b) the maintenance of variation in a sexually selected male trait and its exaggeration across generations (i.e. a long-term effect). Compared to previous theoretical models on the evolution of male traits through sexual selection (e.g. Iwasa & Pomiankowski, 1995; Houle & Kondrashov, 2002; Muniz & Machado, 2018; but see Bailey & Moore, 2012), we innovate by explicitly investigating the effect of within-population variation in female mating preferences.

2.2 | Simulation design

In our IBM, males are characterized by a sexually selected trait z , and females are characterized by two components of their preference

function: a preference, p , and a preference strength, s (all symbols used in the simulations are described in Table 1). In our simulations, female mate choice is probabilistic, and females assess potential mates sequentially (i.e. one at a time), deciding whether to mate or not. The probability that a female i mate with a male j , P_{ij} , can be described by two probabilistic functions with different shapes: (a) open-ended and (b) closed preference (Figure 1). We ran separate sets of simulations in which females had both shapes of preference function, but within each population all females had the same shape of preference function.

The open-ended probabilistic function in our model is a sigmoid describing a female's preference for males with higher z values. This function has two parameters: an intercept and a slope (Equation 1). The intercept p_i is the value of the female preference above which a male has 50% probability of being accepted, whereas the slope s_i is the preference strength that determines the steepness of the sigmoid (Figure 1a–c). The equation describing the open-ended preference function is:

$$P_{ij} = \frac{1}{1 + \exp(-s_i \cdot (z_j - p_i))}. \quad (1)$$

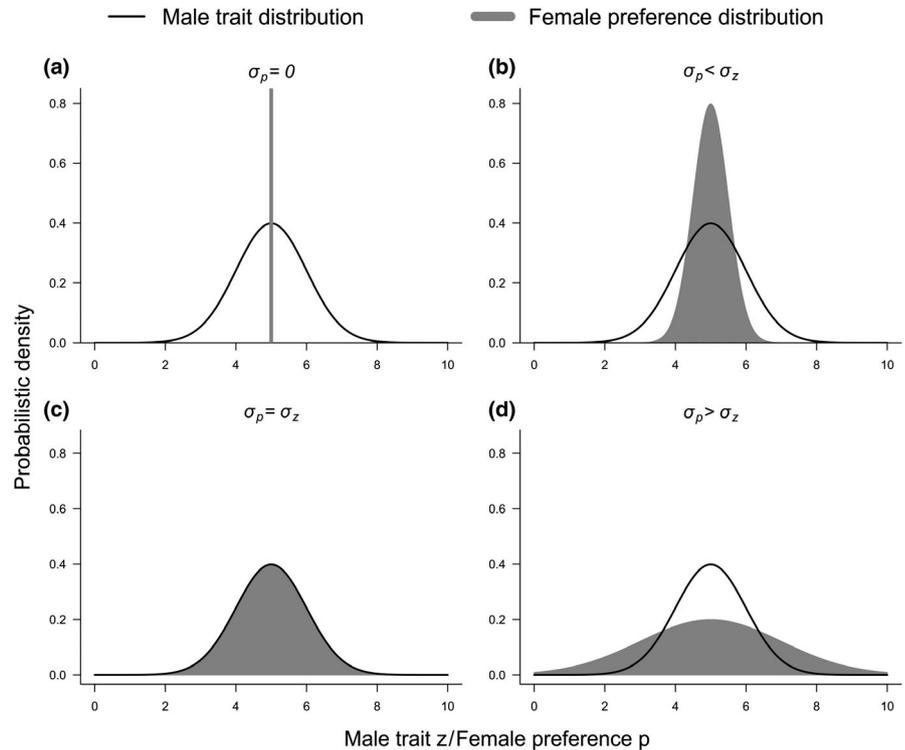
The closed probabilistic function in our model function is bell-shaped and describes female's preference for males with intermediate trait values. This function has two parameters: an intercept p_i and a slope s_i (Figure 1d–f). Potential mates with trait values higher or lower than the female's own preference have an equally increasing chance of being rejected, according to the equation:

$$P_{ij} = \exp(-s_i \cdot (z_j - p_i)^2). \quad (2)$$

Here, a female will certainly mate when $p_i = z_j$, but when $p_i \neq z_j$ she may or may not mate according to her preference strength, s_i . In both preference functions, once a female mate, she stops assessing other males. In our simulations, we allowed each female to assess up to 100 males, so that if a female rejected the first 99 males assessed, she was assigned to mate with the 100th male, regardless of his trait value. Contrary to females, we allowed males to mate as many times as females chose him in each simulation, which is a common pattern in polygynous species (Dewsbury, 2005).

We assigned an initial trait (z) value to all $j = 1, \dots, 1,000$ males from each population by sampling from a Gaussian distribution with population mean equal to φ and standard deviation (σ_z) equal to 1 (Figure 2). All females in the population also have a z value that is not expressed in their phenotypes but is inherited by their offspring (daughters and sons). Individual preference (p_i) and preference strength (s_i) values were assigned to all $i = 1, \dots, 1,000$ females from each population by sampling from a Gaussian distribution with population mean preference (p_{mean}) equal to the mean male trait φ and mean preference strength (s_{mean}) equal to 2. Mean female preference is equal to the mean male trait z , a pattern that has already been reported in some empirical studies (e.g. Gerhardt, 1991). To test the sensibility of our results to this scenario, we also run simulations in

FIGURE 2 Frequency distribution, in the population level, of sexually selected male trait values z (solid black line) and female preference values p (grey shade). In our simulations, there was a control simulation with no variation in female preference (a), and simulations in which the magnitude of within-population variation in the female preference could be lower (b), equal (c) or higher than the variation in the sexually selected male trait z (d)



which mean female preference was different to mean male trait. The results were qualitatively similar and are presented in Appendix S6.

We used a full factorial design to run four types of simulations: (a) open-ended function and within-population variation in preference (Figure 1b); (b) open-ended function and within-population variation in preference strength (Figure 1c); (c) closed function and within-population variation in preference (Figure 1e); and (d) closed function and within-population variation in preference strength (Figure 1f). We also had a control simulation (with no within-population variation in female mating preferences) for open-ended (Figure 1a) and closed preference functions (Figure 1d). We stress that females from the same population always chose their mates according to the same shape of preference function.

For each type of simulation, we established five different values of standard deviation in female preference σ_p (0, 0.25, 0.5, 1.0 and 2.0; see Table 1) or standard deviation in female preference strength σ_s (0, 0.1, 0.2, 0.4 and 0.8; see Table 1). Any value of σ_p or σ_s above zero implies that there is within-population variation; otherwise, a value of σ_p or σ_s equal to zero implies no within-population variation in preference or preference strength and thus can be regarded as a control simulation (Figure 2a).

Finally, female preference p and the male trait z are in the same scale; thus, each unit of standard deviation in p is equivalent to one unit of standard deviation in z . When $\sigma_p < \sigma_z$, within-population variation in female preference is smaller than within-population variation in the male trait (Figure 2b). When $\sigma_p = \sigma_z$, within-population variation in female preference is equal to within-population variation in the male trait (Figure 2c). This latter scenario has already been empirically described for at least two species of treefrogs in which females select males based on acoustic properties of their callings

(Gerhardt, 1991; Neelon et al., 2019). Finally, when $\sigma_p > \sigma_z$, within-population variation in female preference is higher than within-population variation in the male trait (Figure 2d). Although we could not find empirical studies describing this scenario, there is experimental evidence that females prefer artificially manipulated trait values that are far beyond the natural range of variation of male phenotypes (e.g. Andersson, 1982; Drăgănoiu, Nagle, & Kreutzer, 2002), which suggests that there is higher variation in female preference than in sexually selected male traits.

2.3 | Short-term simulations

To explore the influence of within-population variation in female mating preferences on the opportunity for sexual selection on males (I_s), we ran a total of 1,000 simulations (a combination of two shapes of preference function, five values of within-population variation in either preference or preference strength and 50 replicates per combination). These simulations lasted one generation, enough for all individuals in each replicate to: (a) be born, (b) mate and (c) die (Figure S1A of Appendix S2). Mate choice was performed by females as described above. For every replicate, we estimated the opportunity for sexual selection using the index I_s , calculated as:

$$I_s = \frac{\sum_{i=1}^N (w_i - \bar{w})^2}{N} \cdot \frac{1}{\bar{w}^2} \quad (3)$$

In this equation, w_i is the reproductive success of each male, \bar{w} is the mean male reproductive success of all males, and N is the total number of males in the population (Wade, 1979). In our simulations,

random mating would generate a value of I_s close to 1, which represents a scenario with no opportunity for sexual selection. Given that we estimated the I_s for only one generation, these results will be referred from now on as 'short-term results'. In addition to the I_s , we characterized sexual selection acting on male trait z by fitting a quadratic regression between male mating success (i.e. number of copulations) and the male trait z for every replicate—the coefficients of these regressions are unstandardized selection gradients (Lande and Arnold 1983). This procedure allowed us to discover if sexual selection in each simulation was directional, stabilizing or disruptive. In populations with an open-ended preference function, we forced the intercept of the curves to be zero (see details in Appendix S3).

We compared the magnitude of the difference between the opportunity for sexual selection I_s in populations with different values of σ_p or σ_s using the Hedge's g , which is a nondimensional metric of effect size calculated as the difference between any pair of means divided by the pooled standard deviation (Hedges, 1981). The Hedge's g is commonly used in meta-analyses, but effect size metrics are also useful for within-study comparisons (see discussion in Nakagawa & Cuthill, 2007). In general, absolute $g < 0.5$ is considered to represent a slight difference, whereas absolute $g \geq 0.8$ is considered to represent a biologically relevant difference (Durlak, 2009). We did not perform standard null-hypothesis statistical tests because they are not an adequate tool to analyse data from simulations. First, the statistical power is too high, and second, any small effect could generate a low and probably significant p-value (see discussion in White, Rassweiler, Samhouri, Stier, & White, 2014).

2.4 | Long-term simulations

To explore the potential implications of within-population variation in preference and preference strength on the evolution of a sexually selected male trait z , we ran simulations for 50 discrete nonoverlapping generations. In each generation, individuals (a) are born, (b) go through natural selection (i.e. viability selection), (c) mate, (d) reproduce and (e) die (Figure S1B of Appendix S2). After being born, all females survive until the reproductive age (i.e. there is no natural selection acting on female survival). For males, however, survival until reproduction is influenced by stabilizing natural selection on the sexually selected trait that, under certain circumstances, may even oppose the influence of sexual selection (as in Muniz & Machado, 2018; Pomiankowski & Iwasa, 1998). Therefore, male survival (V_j) can be described as:

$$V_j = \exp(-\gamma \cdot (z_j - \varphi)^2), \quad (4)$$

where φ describes the optimum male trait value favoured by natural selection. Thus, the viability of a certain male is lower when the difference between z_j and φ is high. In our simulations, mean male trait value in the first generation was equal to the optimum value (mean $z = \varphi = 5$) and then allowed to evolve. We kept parameter φ constant through generations. The parameter γ describes the

intensity of natural selection acting on trait values different from the optimum. For instance, higher values of γ describe stronger natural selection, that is a greater decrease in survival for males with z_j values away from φ . We set parameter γ to be either equal to 0.20 or 0.05, and both values are within the range of empirical values reported for phenotypic selection on quantitative traits in the wild (reviewed by Kingsolver et al., 2001). Given the patterns we found for both values of γ were qualitatively similar, we focused on describing the results below only for high intensity of natural selection (i.e. $\gamma = 0.2$). The results for low intensity of natural selection are presented in Appendix S4.

After natural selection acts on males, females choose their mates as described in the short-term simulations and reproduction occurs. Precisely, each female produces one daughter and one son, so that each male that managed to mate leaves one daughter and one son per mating. Thus, the total population size and sex ratio (1:1) do not change through generations. After reproduction, all adult individuals die, and their offspring go through the same life cycle. The trait value z of each offspring k is inherited from both parents i and j and is calculated as:

$$z_k = \frac{z_i + z_j}{2} + \varepsilon(0, r), \quad (5)$$

where ε describes the uncertainty related to genetic recombination and mutation. This is a simplified way to model the inheritance and evolution of a continuous male trait as if it was influenced by many small-effect alleles, and it is comparable to quantitative genetic models (Falconer, 1960). Values of ε were sampled from a Gaussian probabilistic distribution with mean equal to 0 and standard deviation r . For simplicity, female values for preference and preference strength are not inherited and thus do not evolve in our simulations (i.e. mean and variation in female preference and preference strength are constant through generations within each replicate). Moreover, we did not set any correlation between female mating preferences and the male trait z .

We ran simulations for a combination of two shapes of preference function (open-ended and closed), five values of within-population variation in either preference or preference strength (Table 1) and 30 replicates per combination. Moreover, the long-term simulations have an additional parameter, γ , which could assume two different values (0.05 and 0.20). Thus, we ran a total of 1,200 simulations. Again, simulations with σ_p or $\sigma_s = 0$ can be regarded as control simulations because there is no within-population variation in female mating preferences. Contrary to the short-term simulations, in which the standard deviation in the male trait z was given by parameter σ_z and was always equal to 1, in the long-term simulations, standard deviation in the male trait z can change through generations. In the first generation of long-term simulations, the standard deviation is given by σ_z , and afterwards, the distribution of z is determined by natural and sexual selection acting on the male trait. Thus, the mean and standard deviation of the male trait (z_{mean} and z_{SD}) at the 50th generation are output variables from the long-term simulations (Table 1).

We compared the values of z_{mean} and z_{SD} for simulations with different values of σ_p and σ_s using the Hedge's g , following the same rationale presented in the short-term simulations. These results, along many generations, will be referred from now on as 'long-term results'.

3 | RESULTS

3.1 | Short-term results: open-ended function

When females chose their mates according to an open-ended function, I_s values were influenced by within-population variation in female preference (σ_p) but only when $\sigma_p > \sigma_z$ (Figure 3a). The simulations with σ_p values ranging from 0.25 to 1.0 had I_s values similar to the control simulations ($\sigma_p = 0$) ($g < 0.3$), but when $\sigma_p = 2$, we found I_s values higher than in control simulations ($g > 0.9$). When we varied female preference strength (σ_s), the I_s remained stable around 1.39 when σ_s was between 0 and 0.2 (Figure 3b; $g < 0.1$), but decreased slightly to 1.36 when $\sigma_s \geq 0.4$ (g values close to 0.5).

Sexual selection always favoured males with higher z values, and the selection regime (i.e. the shape of the selection gradient) was similar for the entire range of within-population variation in

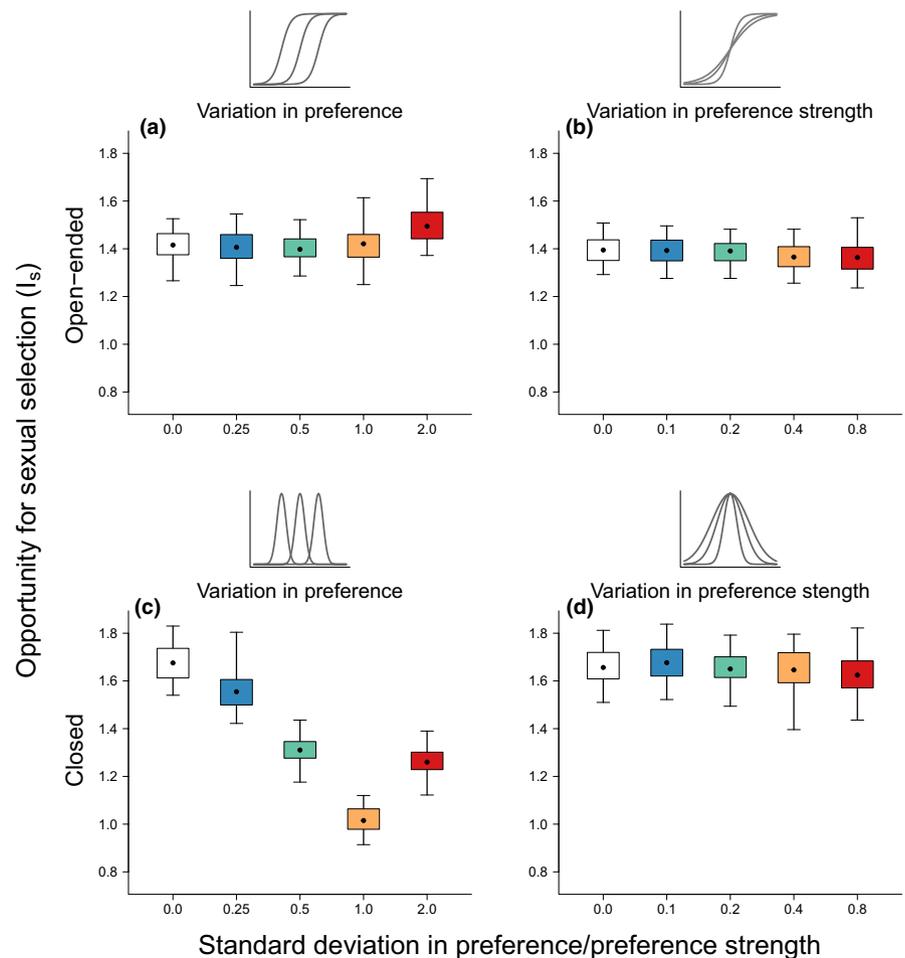
preference σ_p values (Figure 4a-e). Regardless of the magnitude of within-population variation in preference strength σ_s , the regime of sexual selection was similar to the control simulations (Figure S5 of Appendix S5).

3.2 | Short-term results: closed function

When females chose their mates according to a closed function, within-population variation in female preference had a strong effect on I_s (Figure 3c, g values > 0.8). In simulations with σ_p values ranging from 0 to 1, I_s values decreased steadily from 1.7 to 1.0. In simulations with $\sigma_p = 2$, the I_s values increased up to 1.3 (Figure 3c). When we varied female preference strength (σ_s), the I_s remained stable around 1.65 regardless of σ_s values (Figure 3d).

The selection regime depended on the σ_p value (Figure 4f-j). For σ_p values ranging from 0 to 0.5, the relationship between male mating success and male trait z (i.e. the selection gradient) was stabilizing (Figure 4f-h); that is, the mating success was much higher for males with z values close to mean female preference. When $\sigma_p = 1$, the stabilizing selection gradient was flatter, so that male mating success was only weakly correlated with z , even though males with trait values close to mean female

FIGURE 3 Influence of four intensities of within-population variation in female preference function on the opportunity for sexual selection (I_s). We simulated females with: (a) open-ended preference function and with within-population variation in preference; (b) open-ended preference function and with within-population variation in preference strength; (c) closed preference function and with within-population variation in preference; (d) closed preference function and with within-population variation in preference strength. Boxplot colours within each graphic represent values of within-population variation in standard deviation of preference (white_[control simulation] = 0, blue = 0.25, green = 0.5, orange = 1.0 and red = 2.0) and preference strength (white_[control simulation] = 0, blue = 0.1, green = 0.2, orange = 0.4 and red = 0.8). In all boxplots, the central black dot represents the mean, the box delimits the second and third quartiles, and the whiskers extend from the minimum to the maximum values



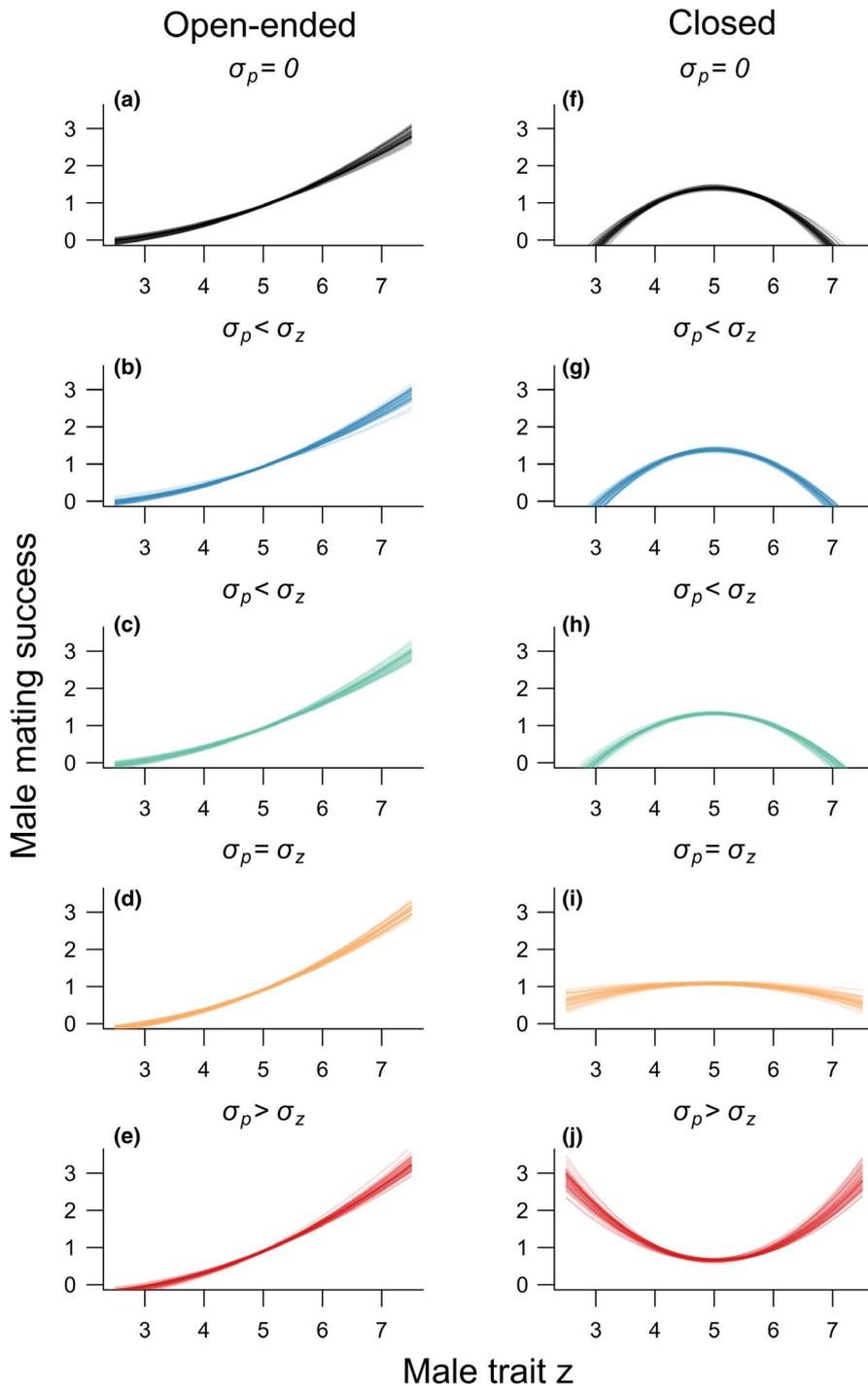


FIGURE 4 Selection gradients obtained from the short-term simulations in which there was within-population variation in female preference (p). Each panel shows the superimposed selection gradients estimated from 50 simulated populations. The left column (a–e) shows simulations in which females had an open-ended preference function, and the right column (f–j) shows simulations in which females had a closed preference function. Colours represent different intensities of within-population variation in female preference (standard deviation): black_[control simulation] = 0, blue = 0.25, green = 0.5, orange = 1.0 and red = 2.0

preference still had slightly higher mating success (Figure 4i). This pattern radically changed when $\sigma_p = 2$, in which the male trait z was under disruptive selection (Figure 4j). This result indicates that male mating success was much higher for males with trait z values extremely higher or lower than mean female preference. Regardless of the magnitude of within-population variation in preference strength σ_s , the regime of sexual selection was similar to the control simulations. All Hedge's g values comparing short-term simulations for open-ended and closed preference functions and for different σ_p and σ_s values are presented in Table S2 of Appendix S5.

3.3 | Long-term Results: open-ended function

When females chose their mates according to an open-ended function and there was within-population variation in female preference, the population mean values of the male trait z (z_{mean}) always increased through generations (Figure 5a). In the simulations with low within-population variation in female preference (i.e. $\sigma_p = 0.25$ and 0.5), z_{mean} was only slightly higher than in the control simulation, in which $\sigma_p = 0$ (Figure 5a; $g < 0.5$). In turn, in simulations with high within-population variation in female preference (i.e. $\sigma_p = 1$ and 2), z_{mean} reached substantially higher values ($g > 1.1$ in

FIGURE 5 Influence of within-population variation in females with open-ended preference functions on the evolution mean and standard deviation of a sexually selected male trait z after 50 generations. We simulated populations in which females varied in their preference (a, c) or preference strength (b, d). Boxplot colours within each graphic represent different intensities of within-population variation in preference (white_[control simulation] = 0, blue = 0.25, green = 0.5, orange = 1.0 and red = 2.0) and preference strength (white_[control simulation] = 0, blue = 0.1, green = 0.2, orange = 0.4 and red = 0.8). In all boxplots, the central black dot represents the mean, the box delimits the second and third quartiles, and the whiskers extend from the minimum to the maximum values

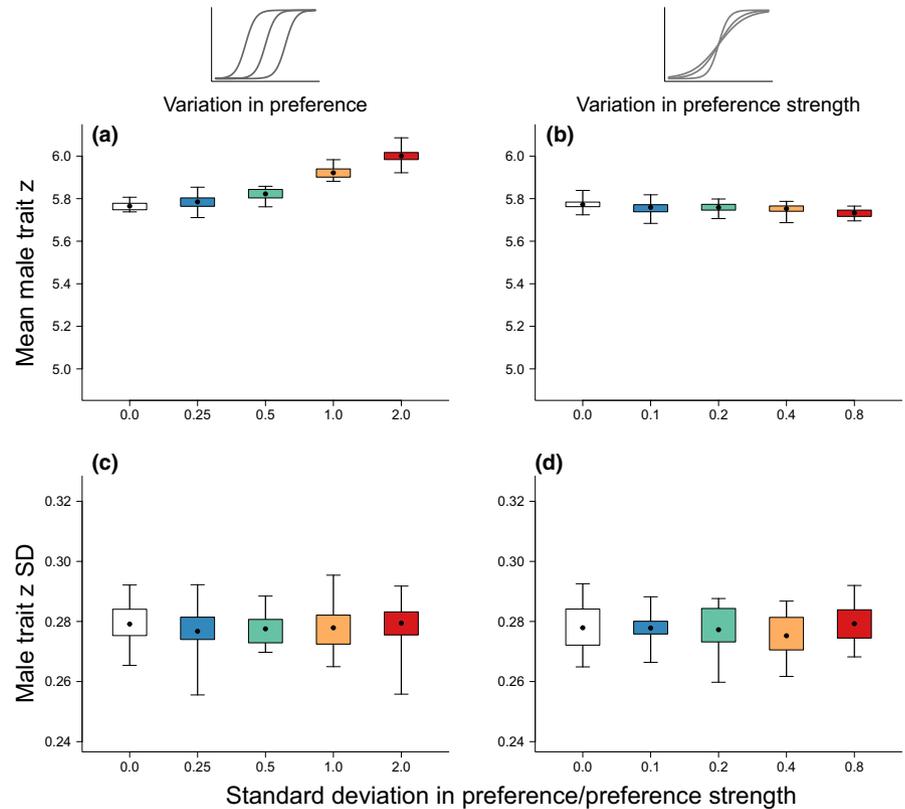
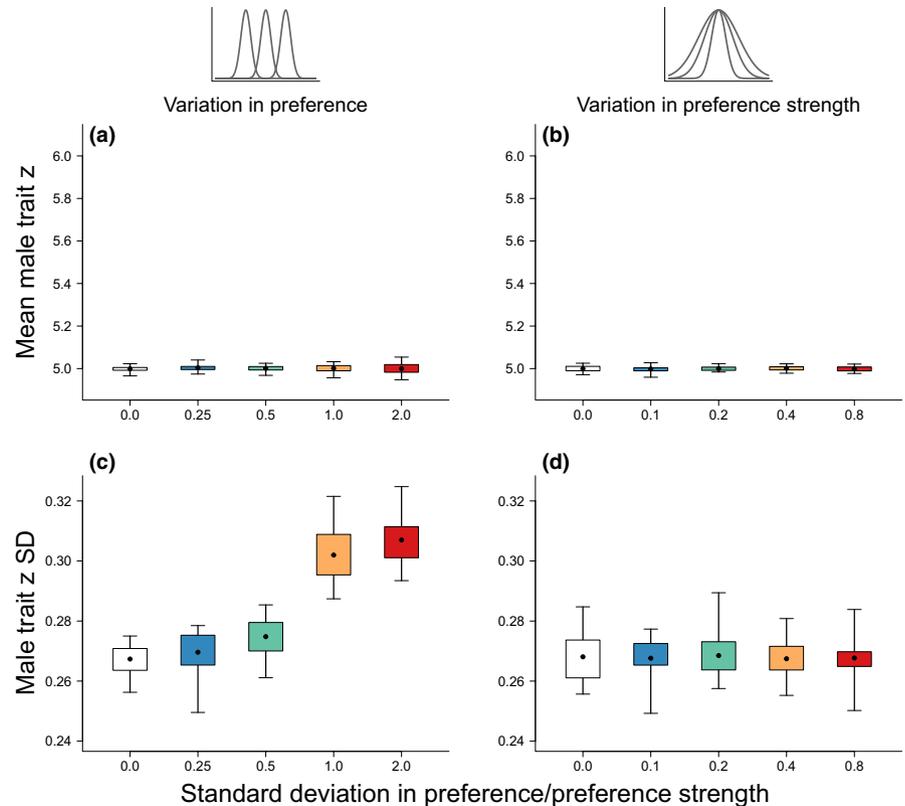


FIGURE 6 Influence of within-population variation in females with closed preference functions on the evolution mean and standard deviation of a sexually selected male trait z after 50 generations. We simulated populations in which females vary in their preference (a, c) or preference strength (b, d). Boxplot colours within each graphic represent different intensities of within-population variation in preference (white_[control simulation] = 0, blue = 0.25, green = 0.5, orange = 1.0 and red = 2.0) and preference strength (white_[control simulation] = 0, blue = 0.1, green = 0.2, orange = 0.4 and red = 0.8). In all boxplots, the central black dot represents the mean, the box delimits the second and third quartiles, and the whiskers extend from the minimum to the maximum values



comparison with control). Moreover, mean variation in male trait z (z_{SD}) decreased from 1.0 (initial condition) to around 0.28 for all values of σ_p (Figure 5c; g values < 0.25). When we varied the preference strength, mean male trait z increased from 5 to around 5.8 for both

the control simulations and all values of σ_s (Figure 5b; g values < 0.3). Additionally, variation in male trait z (z_{SD}) decreased through generations, but final values were similar between control and all σ_s values (Figure 5d; g values < 0.3).

3.4 | Long-term results: closed function

When females chose their mates according to a closed function and there was within-population variation in female preference, mean male trait z_{mean} remained around 5.0 through generations for all values of σ_p (Figure 6a; g values < 0.38). Moreover, mean variation in male trait z (z_{SD}) decreased from 1.0 (initial condition) to around 0.27 both in the control and in the simulations with low within-population variation in preference (i.e. $\sigma_p = 0.25$ and $\sigma_p = 0.5$; Figure 6c). In simulations with high within-population variation in preference (i.e. $\sigma_p = 1.0$ and $\sigma_p = 2.0$), variation in male trait z (z_{SD}) was much higher than in the control simulations (Figure 6c, g values > 1.8). When we varied the preference strength, there was no evolutionary change in mean male trait z through generations regardless of the value of σ_s (Figure 6b, g values < 0.25). Similarly, variation in male trait z (z_{SD}) for all σ_s values was similar to the control (Figure 6d, g values < 0.3). All Hedge's g values comparing long-term simulations for open-ended and closed preference functions for different σ_p and σ_s values are presented in Tables S3 and S4 of Appendix S5.

4 | DISCUSSION

Contrary to a widely accepted expectation, we found that within-population variation in female preference and preference strength does not necessarily reduce the opportunity for sexual selection on males (Figure 3). As we are going to discuss in further detail below, this reduction occurred only when the preference function was closed and females varied in their preference, rather than preference strength (Figure 3c). Moreover, in some instances, variation in female preferences can even increase the opportunity for sexual selection. The results of our long-term simulations do not fully support another widely accepted expectation, which states that variation in female mating preferences maintains variation in sexually selected male traits. Variation in the sexually selected male trait was only higher than in the control simulations (i.e. with no within-population variation in female preference) in very specific conditions: when the preference function was closed and females showed high ($\sigma_p \geq 1$) variation in preference (Figure 6c). Taken together, these results clearly indicate that the effects of within-population variation in female preference function on the opportunity for sexual selection and evolution of sexually selected male traits depend on the interaction between three factors: (a) if variation occurs in preference or preference strength, (b) the type of the female preference function (i.e. open-ended or closed) and (c) the magnitude of within-population variation in the preference functions.

Within-population variation in female preference affected the opportunity for sexual selection, but this effect differed according to the type of the preference function and the magnitude of within-population variation in the preference functions. When females had an open-ended preference function, males with high values of the sexually selected trait were always favoured. The opportunity for sexual selection differed from that of control simulations only when

variation in female preference was higher than variation in male trait (Figure 3a). This happened because males with extremely high trait values are favoured in two different ways. First, they always have a high mating probability with all females in the population (Figure 1b). Second, when variation in female preference is higher than variation in male trait, there are a large number of females with extremely high preference values, which mate only with males with extremely high trait values (Figure 1b). Because these males are rare, they accumulate a disproportionate number of copulations. Thus, given an open-ended preference function, high within-population variation in female preference can intensify the directional selection on the male trait and increase the opportunity for sexual selection—a result that contrasts with previous verbal expectations (reviewed by Jennions & Petrie, 1997; Widemo & Sæther, 1999). Moreover, in our long-term simulations, an open-ended preference function always resulted in exaggeration of the male trait, with values above the optimum favoured by natural selection (Figure 5a,b). This is the classical situation in which sexual selection favours male trait exaggeration, whereas natural selection restricts it (reviewed by Kokko, Jennions, & Brooks, 2006). An interesting result from our simulations was that mean male trait after 50 generations was higher than control simulations only when variation in female preference was high (Figure 5a). This finding indicates that the exaggeration of the sexually selected trait depends on both the type of the preference function and the magnitude of variation in female mating preferences.

Previous studies have proposed that the sexual selection regime acting on males depends mostly on the shape of the female preference function (Edward, 2014): (a) for a positive open-ended preference function, selection is directional and males with extreme trait values in one side of the distribution are favoured (e.g. Drăgănoiu et al., 2002; Pauers, McKinnon, & Ehlinger, 2004); (b) for a closed preference function, selection may be stabilizing when the mean values of female and male distributions are equal so that males with intermediate trait values are favoured (e.g. Kilmer et al., 2017), and (c) for U-shaped preference function (a type of open-ended preference function), selection is disruptive and males with extreme trait values in both sides of the distribution are favoured (e.g. Stelkens et al., 2008). Here, we demonstrated that the sexual selection regime acting on males depends not only on the shape of the preference function, but also on the magnitude of variation in female preference (Figure 4). In our short-term simulations, we found that males were under stabilizing sexual selection in populations in which the preference function was closed and within-population variation in female preference was lower than or equal to variation in the male trait (Figure 4f–i). However, when the preference function was closed and variation in female preference was higher than variation in the male trait, males were under disruptive sexual selection (Figure 4j). These findings exemplify how sexual interactions between individuals can generate unexpected patterns at the population level (e.g. McDonald & Pizzari, 2018; Theraulaz, Gautrais, Camazine, & Deneubourg, 2003). If one were to detect stabilizing and disruptive selection regimes in two different populations of the same species, it would not be obvious that these two selection regimes could be

generated by females with exactly the same closed preference function, but differing only in the amount of within-population variation in their preference.

How could high within-population variation in female preference lead to disruptive selection? When the preference function is closed and variation in female preference is higher than the variation in the sexually selected male trait, there are a relatively high number of females with extreme preference values. However, only a few males in the population have trait values high or low enough to match these extreme preference values (Figure 2d). Thus, these rare males accumulate matings with those relatively common females with extreme preference values. At the same time, there are many more males with average trait value than females that prefer to mate with them. As a result, the mating success of males with extreme trait values is higher than the mating success of males with trait values close to the average. This mechanism causes the disruptive selection gradient observed in Figure 4j. Disruptive selection is known to promote and maintain within-population variation in several naturally selected traits (e.g. Bolnick & Lau, 2008; Calsbeek & Smith, 2008; Grant, 1985; Hendry, Huber, De Leon, Herrel, & Podos, 2009; Martin & Pfennig, 2009; Siemens & Mitchell-Olds, 1996; Smith, 1990). However, empirical examples of disruptive selection promoting and maintaining within-population variation in sexually selected traits are relatively scarce (e.g. Greene et al., 2000; Sappington & Taylor, 1990; Shumate, Teale, Ayres, & Ayres, 2011). Our long-term simulations add to these few empirical studies showing that disruptive selection promoted exclusively by within-population variation in female preference can maintain high variation in a sexually selected male trait (Figure 6c).

In the simulations with variation in preference strength, the open-ended preference function always created directional sexual selection favouring high male trait values (Figure 4). Contrary to what we found for variation in preference, increasing variation in female preference strength slightly decreased the opportunity for sexual selection (in the short-term simulations) and also the exaggeration of the male trait (in the long-term simulations). This result is in accordance with previous verbal expectations, showing that variation in at least one aspect of female mating preferences, namely preferences strength, indeed reduces the sexual selection acting on males (reviewed by Jennions & Petrie, 1997 and Widemo & Sæther, 1999). In a study in which different populations of several animal species were investigated, the diversification of sexually selected male traits was influenced mainly by divergence in preference rather than preference strength (Rodríguez, Boughman, et al., 2013). This result provides empirical support for the notion that the role of preference strength on the intensity of sexual selection and evolution of sexually selected male traits is less important than the effect of preference.

The pattern we reported here for the simulations with variation in preference strength may be a consequence of the directional (and asymmetrical) nature of the open-ended preference function (Figure 1a–c). Increasing variation in preference strength creates some females with high preference strength values (i.e. females with

steep preference functions), as well as some females with low preference strength values (i.e. females with shallow preference functions). Females with shallow preference functions are more likely to mate with males with lower trait values in open-ended functions, but the presence of more females with steep preference functions apparently has little effect on the mating success of males with higher trait values. Thus, the presence of females with shallow preference functions in populations with an open-ended preference function creates more mating opportunities for males with low trait values, decreasing the variation in male mating success and thus the opportunity for sexual selection. However, when the preference function was closed, increasing preference strength produced no consistent effect on the opportunity for sexual selection nor on the exaggeration of the male trait (as empirically reported by Brooks & Endler, 2001). We argue that this pattern is caused by the symmetrical nature of the closed preference function. Females with a shallow preference function are more likely to mate with males of both lower and higher trait values, whereas females with steep preference functions are more likely to mate with males closer to the preference value. Thus, in the simulations with closed function, the presence of females with both shallow and steep preference functions cancels out and the opportunity for sexual selection remains unchanged.

5 | CONCLUSION

Since the seminal review on mate choice by Jennions and Petrie (1997), variation in female mate choice and in different components of preference functions has been widely recognized. In our study, we specifically address two of these components: preference and preference strength (*sensu* Kilmer et al., 2017). These two components are expected to vary independently from each other, and indeed, there is empirical evidence supporting this assumption (Rodríguez, Hallett, et al., 2013, but see Neelon et al., 2019). Here, we showed that variation in these two components can have different effects on the opportunity for sexual selection and the evolution of male traits. The main conclusion from our simulations is that to make predictions on the effect of within-population variation in female preference, it is important to know the shape of the preference function, if females vary in their preference or preference strength, and the magnitude of this variation. Although there are many reported cases of within-population variation in female mate choice, there are not enough studies measuring the female preference function to know which of the two shapes (open-ended or closed) is more frequent in nature (Table S1). Moreover, for almost all species studied so far, there is no information on the magnitude of variation in female preference (but see Gerhardt, 1991; Neelon et al., 2019; Rodríguez, Hallett, et al., 2013). Thus, it is currently difficult to say which of the scenarios we simulated here is the most common in natural populations. Therefore, we encourage empiricists to perform mate choice experiments that allows one to (a) describe the female's preference function and (b) estimate variation in both male traits and female preferences (see guidelines in

Kilmer et al., 2017; Wagner, 1998). If these requirements are met, more accurate predictions can be made about the direction and intensity of the sexual selection and about the evolution of sexually selected male traits.

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CONFLICT OF INTERESTS

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

C.H.M., D.G.M. and G.M. involved in conceptualization, methodology, writing—original draft and writing—review and editing. D.G.M. involved in investigation (simulations), made formal analysis and curated the data. C.H.M. and D.G.M. made visualization. D.G.M. and G.M. supervised the study. C.H.M. made project administration.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Scripts will be available at GitHub upon manuscript acceptance.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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