

The evolution of age-specific choosiness when mating

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Abstract

Mate choice is a crucial element of many processes in evolutionary biology. Empirical research has shown that mating preference and choosiness often change with age. Understanding the evolutionary causes of patterns of age-specific choosiness is challenging because different mechanisms can give rise to the same pattern. Instead of focusing on the optimal age-specific choosiness strategy given fitness trade-offs, we approach this question from a more general standpoint and ask how the strength of selection on choosiness changes with the age at which it is expressed. We show that the strength of selection on a modifier of choosiness at a given age depends on the relative contribution of this age class to the pool of offspring but does not depend directly on the strength of selection on fitness components at the age affected by the modifier. We illustrate our results by contrasting two life histories from the literature. We further show how mutation–selection balance at the choosiness locus can shape age-specific choosiness. Our results provide new insights for understanding the evolution of choosiness throughout life, with implications for understanding the evolution of mate choice and reproductive isolation.

KEYWORDS

assortative mating, life history, senescence, sexual selection, theory

1 | INTRODUCTION

Mate choice is widely documented and has been the focus of a large theoretical and empirical corpus (see reviews in, e.g. Andersson, 1994; Andersson & Simmons, 2006; Rosenthal, 2017). Mate choice can be a crucial element of many processes in evolutionary biology, including the adaptation of populations to novel environments (reviewed in Candolin, 2019), the evolution of conspicuous traits (e.g. Amundsen & Forsgren, 2001) and speciation (Endler & Houde, 1995; Kirkpatrick & Ravigné, 2002; Servedio & Boughman, 2017). Mate choice is defined by two properties, the preference function and choosiness (the strength of preference), both of which have been documented to vary at different scales (e.g. Jennions & Petrie, 1997; Rosenthal, 2017).

Empirical research documents that mating preferences and choosiness change with age (see, e.g., 9.4.4 in Rosenthal, 2017 and

references therein). For example, choosiness has been shown to increase (Wang et al., 2014), to decrease (e.g. Mack et al., 2003; Moore & Moore, 2001) or to fluctuate (Uetz & Norton, 2007) with age depending on the organism studied. Although the evolutionary causes of such age-specific patterns in choosiness are unknown, some theoretical work has explored the possibility that different trade-offs between the costs and benefits of being choosy might result in different optimal patterns of choosiness (e.g. Etienne et al., 2014; Henshaw, 2018). The role of age as a factor of variation in the above trade-off has scarcely been investigated. Though not focusing on age per se, Henshaw (2018) showed that, for organisms choosing their mate only once, the optimum choosiness is expected to decrease when the time window for mating narrows (the “wallflower effect”, De Jong & Sabelis, 1991). Sozou and Seymour (2003) investigated the age-specific optimal strategy of accepting a mate in a time-delay model. In their model, extrinsic

mortality and physiological state (e.g. senescence) determine the fitness benefits and costs of waiting to find a better partner. They found that middle-aged adults would wait longer before accepting a mate than young and old adults. Under their assumptions, middle-aged adults would have a moderate physiological decline and a good evaluation of the external hazard whereas old adults would be physiologically deteriorated (high intrinsic mortality hazard) and young adults would have a poor evaluation of the external risks (potentially high).

These results are interesting, but understanding the evolutionary causes of patterns of age-specific choosiness remains challenging. Indeed, different mechanisms can give rise to the same pattern (see discussion in Mack et al., 2003). For example, suppose we observe a decline in choosiness with age in females. One possible explanation is that this pattern is due to increased reproductive effort at late ages. In particular, if choosiness is costly, then low choosiness would be optimal at late ages when residual reproductive value is low (Charlesworth & Leon, 1976). In this case, the exact pattern of age-specific choosiness would depend on the specific assumptions of the trade-off between choosiness and other fitness components. An alternative explanation, however, is that because the strength of selection is weaker on traits expressed at later ages, the decline in choosiness might be due to nonadaptive senescence through the accumulation of mutations with age-specific (deleterious) effects on choosiness.

These considerations suggest that it would be worthwhile to approach the question from a more general standpoint, and to simply ask how the strength of selection on choosiness changes with the age at which it is expressed, much like Hamilton (1966) did for life-history traits. Such results would not only allow an understanding of how optimal trade-offs across ages play out and can be reached by evolution, but they would also speak to nonadaptive explanations like mutation accumulation.

In this study, we take such an approach and derive expressions analogous to those of Hamilton (1966), but that describe the strength of selection on choosiness expressed at different ages. We model a general mate preference strategy where only females are choosy. Our results build on previous theory on the evolution of choosiness (Otto et al., 2008; Servedio, 2011) and of age-structured populations (Charlesworth, 1994). We assume that there is no direct selection on choosiness, that is it does not affect the vital rates, but that choosiness evolves through sexual selection on the mating traits. Theory shows that indirect selection on choosiness occurs in a wide range of scenarios (Aubier et al., 2019; Cotto & Servedio, 2017; Kirkpatrick, 1982; Lande, 1981; Rowell & Servedio, 2009). We therefore expect the evolutionary mechanisms that we highlight to be relevant in many more complicated biological situations.

2 | METHODS

For simplicity, we assume that individuals are haploid and express a trait that can be under both natural selection (i.e. affecting some

survival rates or fecundities in the life cycle) and sexual selection (i.e. it is used as a criterion for mating preference; see below). Sexually selected traits that are also under natural selection (often labelled as “magic traits” Gavrillets (2004)) favour the evolution of reproductive isolation and have commonly been modelled in speciation theory. Empirical studies further suggest that such traits are prevalent (Servedio et al., 2011). The population is assumed to be polygynous, where females choose males for mating, and where all females have the same mating success. There is thus no sexual selection on females but female mate choice induces sexual selection on males. Finally, for ease of exposition, we assume that individuals are simultaneous hermaphrodites. This assumption simplifies the description of the role of each sex on the evolutionary dynamics at the locus under consideration. The mathematical results below remain unchanged for populations with distinct males and females, and where only the female portion of the population is tracked, but the biological interpretation of the results is more straightforward in the case of hermaphrodites.

2.1 | Mating preference

We assume that when in the female role an individual expresses a mating preference for individuals in the male role that display some phenotype j , and define α_x to be the relative strength of this preference (i.e. choosiness) exhibited by an age- x female. Specifically, if p_j denotes the frequency of phenotype j in the population, then the probability, M_{ij}^x , that an age- x female with phenotype i mates with a male having phenotype j is defined to be

$$M_{ij}^x = \frac{(1 + \alpha_{x,ij})p_j}{\sum_k (1 + \alpha_{x,ik})p_k}, \quad (1)$$

Thus, when an individual is acting as a female, its mate choice affects the frequency of different genotypes among her offspring. We make no a priori assumption on the system of preference, which could be, for example, phenotype matching or condition-dependent preference if there is local adaptation. Notice that if $\alpha_{x,ij} = 0$ for all j then females mate randomly, choosing males in proportion to their frequencies in the population, and larger values of $\alpha_{x,ij}$ correspond to a stronger preference for males with phenotype j .

2.2 | Life history

We allow an individual's vital rates to depend on its genotype, but we assume that mate choice for an individual acting as a female does not affect her fecundity. Choosiness is thus not under direct selection. We denote by $b_{x,j}$ the mean fecundity of such a female of age- x and phenotype j . Likewise, we use $s_{x,j}$ to denote the probability of an individual of genotype j surviving from age- x to age- $x + 1$. In our notation, we assume that population census is performed immediately before reproduction, and therefore, fecundities include first-year

survival, s_{0j} . Following classical notation for age-structured population models, we further define $l_{xj} = \prod_{y=0}^{x-1} s_{yj}$ to be the probability that a genotype j individual survives from conception to age- x (Charlesworth, 1994).

3 | RESULTS

In what follows, we consider two different types of genetic architecture for the phenotype under mating preference and the corresponding choosiness. The mathematical analysis of simplified situations provides our main and most general conclusions. We illustrate and discuss these conclusions with numerical examples.

In the numerical illustrations, we model life cycles with two (reproducing) age classes corresponding to young and old adults. We contrast an insect-like and a fish-like life cycle (see Appendix S1). In the insect-like life cycle, most offspring are contributed by young adults, whereas old adults contribute most to the total progeny in fish. We additionally provide an example with three age classes in Appendix S4.

3.1 | Single locus pleiotropic for choosiness and trait

We first consider the case of a single locus that is pleiotropic for the trait under mating preference and choosiness. In other words, an allele at this locus determines both the trait value and the female choosiness for preferred males. Note that in this section, there is no assumption on natural selection. That is, the intrinsic growth rate of each genotype (when alone, or under random mating) can differ.

We assume that the trait allele A with corresponding female choosiness for preferred males with phenotype j (either A or a), $\alpha_{x,Aj}$, is fixed in the population and consider the fate of a rare mutant allele a . Because allele a is rare, individuals carrying this allele will mate only with resident A -carrying individuals. Under this assumption, to first order in the frequency of allele a , the growth rate, $\lambda_{a|A}$, of a when found in a population dominated by allele A , satisfies the following Euler-Lotka equation (see Appendix S2):

$$1 = \sum_{x=1}^{\infty} \lambda_{a|A}^{-x} l_{x,a} m_{x,a} \tag{2}$$

where $m_{x,a}$ is the expected fertility of an a -carrying individual of age- x . In particular, $m_{x,a}$ is given by

$$m_{x,a} = \frac{b_{x,a}}{2} + \sum_{y=1}^{\infty} u_y R_{y,A} \frac{b_{y,A}}{2} \tag{3}$$

The first term corresponds to the reproductive output when the a -carrying, age- x individual is acting as a female. In this case, it will produce a total of $b_{x,a}$ offspring, only half of which will carry the a allele (since all matings are with resident, A -carrying males). The second term corresponds to the reproductive output when the

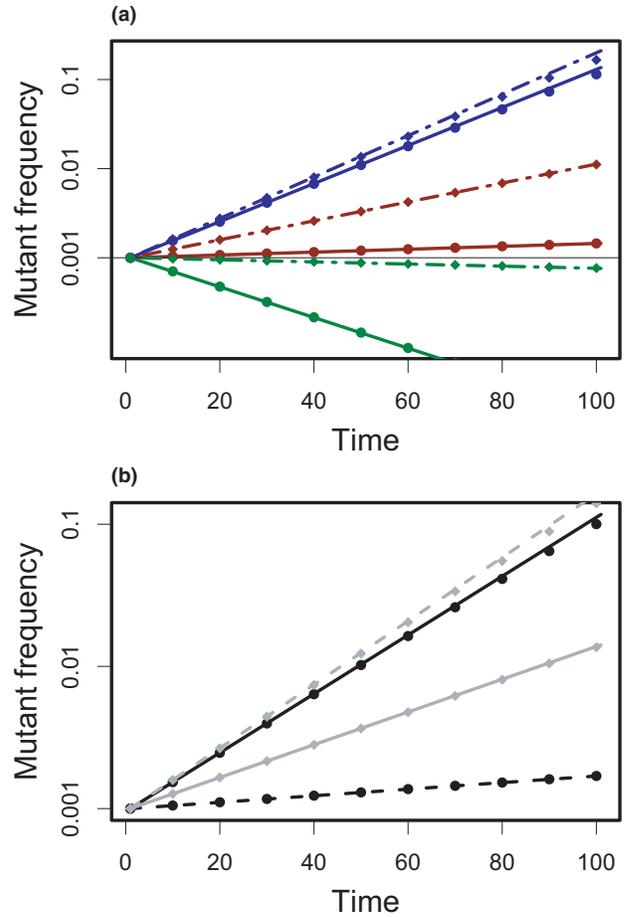


FIGURE 1 Dynamics of the mutant allele a for different mating schemes and for two contrasted life histories. The initial frequency of the mutant allele a is $p_a = 0.001$. Dots and diamonds represent the expectation from Equation (2) for the insect and fish life cycles, respectively. Both life histories are provided in Appendix S1. The mutant allele a confers the survival probability at age 1 $s_{1,a}$ as given in App. 1, whereas allele A provides $s_{1,A} = 0.95s_{1,a}$ (0.89 and 0.76 in the insect and fish life cycles resp.). The mutant allele thus improves survival relative to the resident allele. Panel A: females of all ages have the same choosiness ($\alpha = 0.1$). Red: random mating, blue: all females prefer mutant a -carrying males, green: phenotype matching (A -carrying females prefer A -carrying males and resp. for allele a). Solid line: insect life cycle, dashed line: fish life cycle. Panel B: All females prefer to mate with mutant a -carrying males and choosiness is age-specific. Full lines: only age-1 females are choosy ($\alpha_{1,a} = 0.1$ and $\alpha_{2,a} = 0$), dashed lines: only age-2 females are choosy ($\alpha_{1,a} = 0$ and $\alpha_{2,a} = 0.1$); grey and black: fish and insect life cycles, respectively

a -carrying, age- x individual is acting as a male. The reproductive output of such a male is determined by the fecundity of the resident female with which it mates. The quantity u_y is the fraction of all females in the resident (A -carrying) population that are of age y , and

we have defined $R_{y,A} = \frac{1 + \alpha_{y,Aa}}{1 + \alpha_{y,AA}}$ which represents the preference of such females for mutant a -carrying males, relative to resident

A-carrying males. These females will produce a total of $b_{y,A}$ offspring, only 1/2 of which will carry the mutant a allele. Summing this over all ages of resident females gives the second term in Equation (3). The mutant allele will increase in *number* provided that $\lambda_{a|A} > 1$ but, for the mutant allele to increase in *frequency* we must have $\lambda_{a|A} > \lambda_A$.

To first order, only the choosiness of resident females affects the growth rate of the mutant allele. Figure 1 shows that Equation (2) provides a good approximation to the growth of allele a , even though slight deviations from the approximation appear when allele a reaches high frequency (≈ 0.1). Note that the sensitivity of the age-specific contribution to the offspring pool to a change in survival in young adults is larger in the fish life cycle than in the insect one (Figure 1).

The effect of the choosiness of resident females on the growth rate of the rare mutant depends on whether it is preferred or not (e.g. if the mutant provides a better condition in the current environment or is deleterious). If the mating system favours the locally best phenotype, sexual selection arising from female mating preferences contributes to promote the fittest allele (and purging deleterious mutations, Figure 1a compare blue and red lines). Phenotype matching, whereby females prefer to mate with males of their own type regardless of whether it is locally adapted (see Kopp et al. (2018) for a review of situations where phenotype matching occurs), provides an interesting alternative. Phenotype matching generates positive frequency-dependent sexual selection. Sexual selection acts against any rare mutant, regardless of its fitness (Figure 1a, green lines). Thus, even though the mutant allele might have a fitness larger than one when alone (i.e. $\lambda_{a|a} > 1$), it can nevertheless have a fitness < 1 when rare compared with allele A (i.e. $\lambda_{a|A} < 1$). This means that, if a mutant allele is to spread in a population dominated by a choosy allele, it needs to provide a large enough fitness advantage to compensate for the cost it endures through the effect of positive frequency-dependent sexual selection.

From Equation (3), we can see that the effect of age-specific choosiness of resident females on the growth rate of a mutant allele depends on the contribution of the choosy age classes to the offspring pool, as measured by $c_{y,A} = u_y b_{y,A} / 2$ (we keep the factor 1/2 in this term to simplify the notations below, without loss of generality). The effect of choosiness on mutant growth is larger when resident females are choosy at the ages contributing the most to the offspring pool (Figure 1b). This conclusion carries over to mutant females, whose choosiness have the strongest effect on the mutant growth rate in the age classes contributing most to the pool of mutant offspring.

This age-specific effect can be further investigated by computing the derivative of the mutant growth rate in the resident population, $\lambda_{a|A}$, with respect to the ratio of resident choosiness for each type at a given age z , $R_{z,A}$ (following Hamilton, 1966). We obtain (see Appendix S2 for the details of the calculation).

$$\frac{\partial \ln \lambda_{a|A}}{\partial R_{z,A}} = c_{z,A} \frac{\sum_{x=1}^{\infty} l_{x,a} \lambda_{a|A}^{1-x}}{\sum_{x=1}^{\infty} x \lambda_{a|A}^{1-x} l_{x,a} m_{x,a}} \quad (4)$$

The second factor on the right-hand side in Equation (4) is similar in form to result 25 in Hamilton (1966). It is the sum of the strengths of selection on each age-specific fecundity (as found in Hamilton, 1966). This second factor does not depend on z nor on the strength of selection on fecundity at age z , but depends on the lifetime moulding of age-specific fecundities by selection (Hamilton, 1966). The first term on the right-hand side highlights that the effect of a change in choosiness of A -carrying females at age z on the mutant growth rate is proportional to the contribution of this age class to the offspring pool, $c_{z,A}$. Consistent with this result, mating preferences of young reproductive females in insects increase the growth of the mutant more than preferences of old females. Conversely, in fish, old females contribute most to the offspring pool such that mating preferences of these females have the strongest effect on the growth rate of the mutant (Figure 1b).

3.2 | Two-locus model

3.2.1 | Mathematical analysis

We now focus on the more general case where different loci code for the trait and for age-specific choosiness (for recent empirical evidence, see Neelon et al., 2019). With sexual selection only (when both alleles at the trait locus have the same vital rates), the growth rate, $\lambda_{m|M}$, of a rare mutation m coding for choosiness $\alpha_{x,m}$ at the modifier locus when found in a population dominated by M must satisfy the Euler-Lotka equation (see Appendix S3):

$$1 = \sum_x \lambda_{m|M}^{-x} l_{x,m} m_{x,m} \quad (5)$$

where fertility $m_{x,m}$ is given by

$$m_{x,m} = \frac{b_x}{2} + \sum_y [u_{y,A} R_{y,A} + u_{y,a} R_{y,a}] \frac{b_y}{2} \quad (6)$$

The form of Equation (6) is identical to that of Equation (3). The first term again corresponds to the reproductive output when the age- x mutant is acting as a female. Likewise, the second term corresponds to the reproductive output when the age- x mutant is acting as a male. And again the reproductive output of such a male is determined by the fecundity of the resident female with which it mates. Now, however, there are two different genotypes of resident females with which such mutant males can mate, namely AM and aM . The quantity $u_{y,A}$ is the fraction of all resident females that are of genotype AM and age y . Recall that female mating preference targets the mating trait (A or a). However, from the choosiness locus point of view, what matters is whether female preference for a given trait results in mating preferentially with males carrying one or the other allele at the choosiness locus (M or m). By analogy with the one-locus case, we call $R_{y,A}$ the indirect preference (resulting from direct preference on the mating trait) of resident M -carrying females for mutant Am males, relative to

resident AM males (defined explicitly below). Similarly, $u_{y,a}$ is the fraction of all resident females that are of genotype aM and age y , and $R_{y,a}$ is the indirect preference of such females for mutant am males, relative to resident aM males. In both cases, such females will produce a total of b_y offspring, only half of which will carry the mutant M allele.

The relative indirect preferences $R_{y,A}$ and $R_{y,a}$ are somewhat more complicated in the two-locus case as compared with the 1-locus case. If we define n_{id} as the number of individuals of genotype kl , then the ratio

$$\frac{n_{Am}(1 + \alpha_{y,AM,A}) + n_{am}(1 + \alpha_{y,AM,a})}{n_{Am} + n_{am}} \quad (7)$$

is the factor by which the mating success of mutant males (i.e. males carrying m) is different from random mating as a result of resident females (carrying M) with trait allele A and age y having a mating preference. Likewise, the ratio

$$\frac{n_{AM}(1 + \alpha_{y,AM,A}) + n_{aM}(1 + \alpha_{y,AM,a})}{n_{AM} + n_{aM}} \quad (8)$$

is the factor by which the mating success of resident males (i.e. males carrying M) is different from random mating as a result of resident females with trait allele A and age y having a mating preference. The relative value of these two ratios is then the indirect preference of A -carrying resident females (with genotype AM) for mutant m males, relative to resident M males; that is,

$$R_{y,A} = \frac{n_{Am}(1 + \alpha_{y,AM,A}) + n_{am}(1 + \alpha_{y,AM,a})}{n_{Am} + n_{am}} \bigg/ \frac{n_{AM}(1 + \alpha_{y,AM,A}) + n_{aM}(1 + \alpha_{y,AM,a})}{n_{AM} + n_{aM}}.$$

In a similar fashion, we also have the indirect preference of a -carrying resident females for mutant m males, relative to resident M males as

$$R_{y,a} = \frac{n_{am}(1 + \alpha_{y,aM,a}) + n_{aM}(1 + \alpha_{y,aM,A})}{n_{am} + n_{aM}} \bigg/ \frac{n_{aM}(1 + \alpha_{y,aM,a}) + n_{AM}(1 + \alpha_{y,aM,A})}{n_{aM} + n_{AM}}.$$

Similar to the one-locus case, the effect of resident choosiness is enhanced when females are choosy at ages with a large contribution to the offspring pool. This is reflected in Equation (6) by the factors

$$u_{y,i} b_y / 2 = c_{y,i} \text{ in the summations } \sum_y u_{y,A} \frac{b_y}{2} R_{y,A} \text{ and } \sum_y u_{y,a} \frac{b_y}{2} R_{y,a}$$

Unlike in the one-locus case, however, the association of the modifier with the trait allele (i.e. linkage disequilibrium) also impacts the effect of resident choosiness. This is reflected by the factors $R_{y,A}$ and $R_{y,a}$ in the above summations. In the special case where there is no linkage disequilibrium, the second sum in

Equation (6) becomes $\sum_y \frac{b_y u_y}{2}$ as would be expected under random

mating: to first order, there is no change in allele frequency at the modifier locus (the change in frequency at this locus resulting from nonrandom mating appears at second order). In general, however, mating preference generates linkage disequilibrium between the trait and modifier loci. The effect of linkage disequilibrium can be described in some limiting cases. When preference is directional, for example all females prefer A -carrying males, and the modifier is always associated with the less-preferred trait allele (e.g. a), it can be easily shown that $R_{y,A} < 1$ and $R_{y,a} < 1$ thus decreasing the growth rate of the modifier. Conversely, a positive association between the preferred trait and the modifier increases its growth rate. These conclusions extend to the case of incomplete linkage disequilibrium. With phenotype matching (that is a -carrying females prefer to mate with a -carrying males and similarly for trait A), sexual selection is positive frequency-dependent. The growth rate of the modifier is thus enhanced when it is in association with the most frequent trait allele. For example, assuming that $p_a \ll p_A$, the term in brackets in equation 6 is proportional to n_{Am}/n_{AM} , which is larger than 1 if the modifier m is mostly associated with the common allele A .

By introducing a new (age-specific) choosiness value, a mutant at the modifier locus triggers changes in the linkage disequilibrium. Insights on how the build-up of linkage disequilibrium depends on age-specific choosiness can be obtained by decomposing this measure in offspring from different mating schemes. Consider the case where females of age y are choosy whereas females in the other age classes mate randomly. We can distinguish between the offspring produced by females with age $x \neq y$ (mating randomly) and the offspring produced by females of age y (mating assortatively). We note $\tilde{c}_y = c_y / \sum_x c_x$ the fraction of offspring contributed from females with

age y , where $c_x = \sum_i c_{x,i}$. The total linkage disequilibrium D in off-

spring at time $t + 1$ is given by $D(t + 1) = X_1(t + 1)X_4(t + 1) - X_2(t + 1)X_3(t + 1)$, where X_{1-4} correspond to genotypes AM , Am , aM , am , respectively. Each $X_i(t + 1)$ can be decomposed as $(1 - \tilde{c}_y)X_{i,r}(t + 1) + \tilde{c}_y X_{i,p}(t + 1)$ corresponding to the fraction of offspring with genotype i from random mating (subscript r) and from preference mating (subscript p). After rearranging, we obtain

$$D(t + 1) = (1 - \tilde{c}_y)^2 D_r + \tilde{c}_y^2 D_p + (1 - \tilde{c}_y) \tilde{c}_y D_{p,r} \quad (9)$$

where D_r and D_p are the linkage disequilibria within offspring from random mating and assortative mating, respectively (the index $t + 1$ has been removed for concision), and $D_{p,r} = (X_{1,r}X_{4,p} + X_{1,p}X_{4,r}) - (X_{2,r}X_{3,p} + X_{2,p}X_{3,r})$. The genotypic frequencies and linkage disequilibrium in offspring issued from females mated assortatively are complex terms. Among offspring issued from females mated randomly, genotypic frequencies are unchanged and the linkage disequilibrium is reduced by recombination r following $D_r = (1 - r)D$.

Equation (9) shows that age-specific choosiness affects the change in linkage disequilibrium through the relative contribution of choosy females to the total offspring pool \tilde{c}_y . Linkage disequilibrium between loci builds up faster when choosy females contribute a lot to the offspring pool. In the particular case where there is no initial linkage disequilibrium, $D = 0$, $D_{p,r} = D_p$ so that $D(t + 1) = \tilde{c}_y D_p$. The build-up of linkage disequilibrium is proportional to the contribution of age class y to the offspring pool, \tilde{c}_y .

3.2.2 | Numerical illustrations

We compare the dynamics of a rare modifier of choosiness, and the mutation–selection balance at the choosiness locus, for the insect-like and fish-like life cycles. Importantly, the numerical analysis does not aim to determine the optimal choosiness value (which has been done elsewhere, e.g. Etienne et al., (2014)), but rather to illustrate the conclusions from the mathematical analysis and their implications.

Mutant dynamics

For simplicity, we investigate the dynamics of a modifier of age-specific choosiness in a random mating resident population. The modifier is initially rare ($p_m = 0.01$) and in linkage equilibrium with the trait locus (Equation (5) does not allow to investigate this scenario, see above). To emphasize age-specific sexual selection at the choosiness locus, we also assumed that there is no selection at the trait locus (but see the one-locus case above). We illustrate the case where all females prefer males with the same trait allele a which is initially relatively rare in the population ($p_a = 0.1$), corresponding for instance to a scenario where an allele improves the ornament without cost on survival or fecundity. We also investigated the case of phenotype matching (see Figure S3) and provide an example with three age classes (Appendix S4) with similar conclusions.

Consistent with our predictions, a modifier of choosiness has the largest impact on the trait frequency when it affects the age class contributing most to the offspring pool (young adults in the insect life history and old adults in the fish life history, Figure 2a). When the resident population mates randomly, the modifier always increases in frequency when it codes for some choosiness. The increase in frequency of the modifier is fastest when it codes for choosiness at the age contributing most to offspring pool (Figure 2b). The choosiness value encoded by the modifier affects quantitatively the dynamics but the relative effect of age remains similar, as long as the effect-size on choosiness does not depend on age (not shown). Choosiness evolves quicker in the age classes contributing the most to the offspring pool (which might vary depending on the species, e.g. insect-like or fish-like life history) than in those with little contribution, irrespective of the preference scheme.

Since there is no direct selection on the choosiness locus, evolution at this locus occurs through linkage disequilibrium with the trait locus. The build-up of linkage disequilibrium is correspondingly

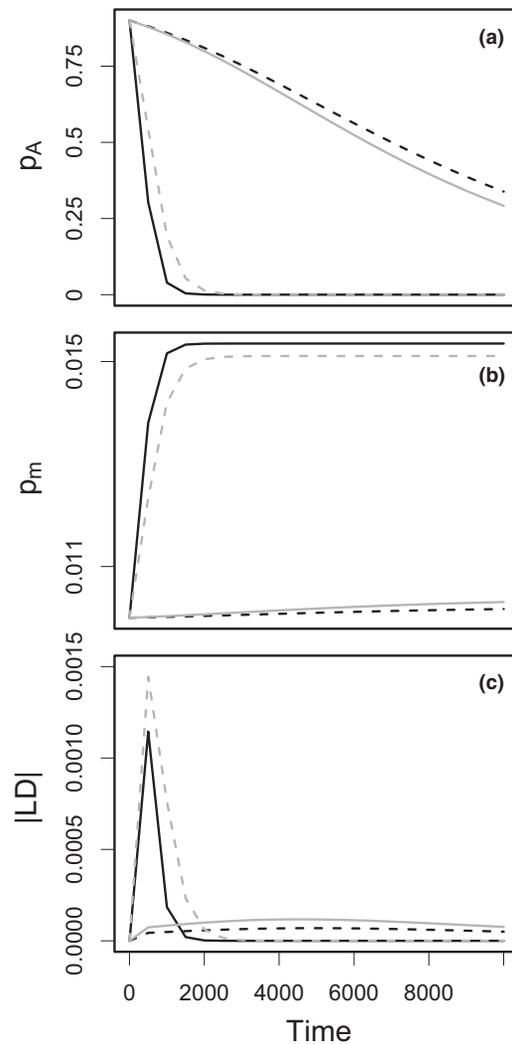


FIGURE 2 Dynamics at the trait locus (a), modifier locus (b) and of the linkage disequilibrium (c) when a modifier of age-specific choosiness m appears in a random mating population with resident choosiness allele M ($\alpha_{.,M} = 0$). The modifier triggers a preference of age- x females for males carrying allele a . The initial frequency of allele a is $p_a = 0.1$. The initial frequency of the modifier is $p_m = 0.01$ and $\alpha_{x,m} = 2$ where x is the age that becomes choosy (the other age class remains random mating). Black and grey: insect- and fish-like life cycles, respectively. Full lines and dashed lines the modifier affects choosiness at age- $x = 1$ and at age- $x = 2$, respectively. The effect of age is reversed in the fish life history as compared to the insect life history

fastest and strongest when the modifier affects the most contributing age classes (Figure 2c). As the frequency of a reaches high frequency (and variance at the trait locus decreases), the linkage disequilibrium decreases.

Mutation–selection equilibrium

Similarly to traits related to adaptation to the local environment (see, e.g., Cotto and Ronce 2014), age-specific variation of the strength of selection on choosiness can affect the ability to purge deleterious

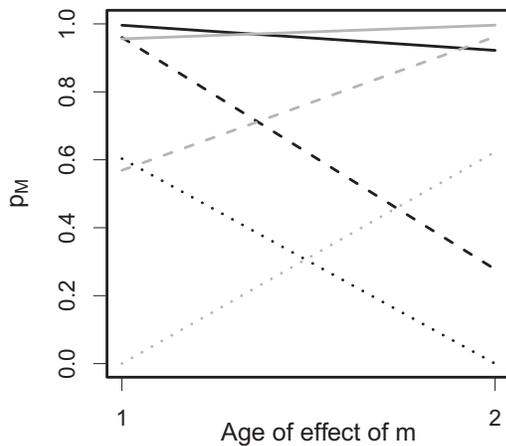


FIGURE 3 Frequency of the choosiest allele (M) at equilibrium mutation–selection as a function of the age of effect of a mutation (m) decreasing choosiness, for different mutation rates μ_{Mm} from M to m . Full line: $\mu_{Mm} = 0.00001$, dashed line: $\mu_{Mm} = 0.0001$, dotted line: $\mu_{Mm} = 0.001$. Allele M codes for the same choosiness in both age classes $\alpha_{\cdot M} = 2$. The mutant allele m decreases choosiness only in age class x , either young ($x = 1$) or old adults ($x = 2$) with $\alpha_{x,m} = 1$. The preference scheme is that all females prefer to mate with a -carrying males. Mutations occur at the trait locus with frequency $\mu_{Aa} = \mu_{aA} = 0.05$. The initial condition is $p_M = p_m = 0.5$ and $p_A = p_a = 0.5$. The simulations are run for 50,000 time units, when equilibrium is reached. Black: insect life cycle and grey: fish life cycle

mutations (theory of mutation accumulation for senescence; Hamilton, 1966; Medawar, 1952). We illustrate this scenario by assuming that most spontaneous mutations occurring with frequency μ_{Mm} decrease choosiness (e.g. if choosiness requires complex receptors). We also implement mutations at the trait locus in both directions (μ_{Aa} and μ_{aA}), to maintain variation.

Consistent with the expectation, the equilibrium mutation–selection for mutations affecting age-specific choosiness depends on the contribution of the age classes to the offspring pool. Selection maintains a high frequency of the choosiest allele in the age classes contributing most to the offspring pool (Figure 3), even under relatively strong mutation rates. At the ages with low contribution to the offspring pool, that is young adults in fish and old adults in insects, high mutation rates at the modifier locus lead to the loss of the choosiest allele. This is because selection is too weak to maintain the association of the choosiest allele with the preferred trait, in the face of recombination and mutations.

4 | DISCUSSION

In this study, we investigated how the strength of selection on choosiness varies with age. Our investigation differs from, and complements, previous studies that have focused on optimization of trade-offs. Trade-off analyses necessarily make specific assumptions about the link between the components of fitness (accounting for the costs and benefits of being choosy) that negatively

covary, whereas our analysis focuses more generally on the age-specific strength of selection acting on mating preferences, much as Hamilton (1966) did for age-specific life-history traits. This thereby provides insights, not only into how selection ought to shape mating preferences that potentially trade-off across different ages, but also into how evolutionary processes can maintain such preferences as well. Our analysis does not depend on the mating scheme, which could be preference for a given phenotype (e.g. with better condition) or phenotype matching, with the aim of unravelling the general mechanisms that occur when age-specific sexual selection operates.

Our main result is that the evolution of age-specific choosiness depends on the contribution of each reproductive class to the offspring pool. We found that the strength of selection on choosiness is stronger for ages with a large contribution to the offspring pool than for those with a small contribution. The contribution of an age class to the offspring pool is proportional to the frequency of this age class, multiplied by its mean fecundity. The numerical illustrations of this result are based on life history of actual species, contrasting a life cycle where young reproductive adults contribute most to the progeny (that we describe as insect-like life cycle) with one where old reproductive adults do (fish-like life cycle). Even though we simplified these life histories to fit in a model with two age classes, the relative contributions of the young and old reproductive adults to the offspring pool follow that of the original life cycle (see Appendix S1). We expect the case where old reproductive individuals contribute most to the offspring pool to be more frequent in species with indeterminate growth. It is likely that nonmonotonous age-specific contributions to the offspring pool, with a maximum contribution at some intermediate ages, is the most common case.

From a theoretical point of view, it is interesting that selection on a modifier of choosiness in a given age class does not depend directly on the strength of selection on the corresponding age-specific fecundity, as measured by the sensitivity of the malthusian growth rate to a change in this trait (Hamilton, 1966). However, Equation (4) shows that selection on age-specific choosiness depends on the strength of selection on fecundity at *all* ages. This result emphasizes that the evolution of age-specific choosiness is tightly linked to the evolution of life history, which eventually determines the age-specific fecundities and the population age structure.

Even though we did not intend to predict the optimal pattern of age-specific choosiness, our results on how evolutionary processes can shape and maintain optimal age-specific choosiness strategies have several implications. First, we predict that the optimal age-specific choosiness value would be reached faster in ages contributing most to the offspring pool. For example, providing that mutations with age-specific effects on choosiness occur, the build-up of reproductive isolation during speciation can be age-specific, with ages contributing the most to the offspring pool evolving strong mating preference quicker than the other age classes. We also predict that when evolution favours an optimal mean choosiness level in the population (e.g. as is predicted by models without age structure), this level would likely evolve as a weighed average of choosiness in each age class, with weights representing the contribution of each age

class to the offspring pool. Furthermore, our results propose that selection is unlikely to be able to optimize choosiness at ages with little contribution to the offspring pool if spontaneous mutations on average decrease choosiness. This is true in particular when choosiness is not under direct sexual selection. Our results thus support the interpretation that observed low choosiness values of the oldest females might well result from senescence (e.g. through the accumulation of mutations with late deleterious effect on sensitivity to signal) rather than from a terminal investment (Moore & Moore, 2001). More interestingly, our results suggest that the prevalent observation that choosiness is low in early reproductive ages (e.g. Uetz & Norton, 2007) might also reflect weak selection on early choosiness. Testing this conclusion further would require an estimation of the expected contribution of each age class to the offspring pool. Overall, weak selection on age-specific choosiness can have major implications to our understanding of the evolution of (incomplete) reproductive isolation (Servodio & Hermisson, 2020).

Our analysis assumes that some mutations have age-specific effects on choosiness. This assumption is supported by the observation that choosiness and mating preference vary with age (see Introduction). Our results on the strength of selection on such mutations depend on a number of simplifying assumptions that we discuss below. The one-locus case corresponds to complete linkage (e.g. physical linkage due to proximity on the chromosome) between the trait and choosiness loci (equivalent to a fully pleiotropic locus). Our analysis of this case does not make any assumption on selection, such that it encompasses cases where choosiness is under direct selection (e.g. choosiness is costly) and where the trait locus is under natural selection. However, our results for the two-locus analysis rely on the assumption that sexual selection is the only evolutionary force (to obtain the form of the Euler-Lotka equation), without natural selection on the trait locus or direct selection on the choosiness locus. Evolution at the choosiness locus occurs through linkage disequilibrium with the trait locus. With natural selection at the trait locus, the growth rate of a modifier of choosiness thus depends on the intrinsic growth rates of the trait alleles with which it is associated. Predictions from models of choosiness evolution by indirect sexual selection in general agree with those from models assuming weak direct selection on choosiness (Kopp & Hermisson, 2008; Schneider & Bürger, 2006). Yet, we expect that variation in direct selection on choosiness with age could affect our results, if such selection dominates the indirect effects we describe. Lastly, our derivations hold under the conditions where the intrinsic growth rate is a valid measure of fitness. Such conditions include the case of density independent growth and that of age-independent density dependence (Mylius & Diekmann, 1995). Density dependence can, however, affect the population dynamics in ways that modify the relevant fitness measure (Mylius & Diekmann, 1995), in turn affecting derivations of the age-specific selection gradients (e.g. Abrams, 1993). The effect of age-specific density dependence on the strength of selection on age-specific choosiness remains to be explored in further studies.

An obvious, but important, conclusion resulting from our analysis is that choosiness should evolve in age-structured population when the mating system generates sexual selection. This result contrasts with most theory on evolution in such structured populations, which typically assumes that mating is random. This is significant because ample empirical evidence suggests that age-specific mate choice is common, both in animals (Andersson, 1994; Rosenthal, 2017) and plants (e.g. Burley & Willson, 2020; Marshall & Ellstrand, 1988). As in unstructured populations, mate choice can affect the evolutionary dynamics in structured populations. For example, given our assumptions, we found that strong choosiness in a population with phenotype matching can hamper the spread of favourable mutations (Figure 1a). The fitness benefits of such mutations have to counterbalance their initial disadvantage resulting from positive frequency dependence in favour of the resident. This result points to the need to consider nonrandom mating in models of adaptation to environmental changes.

Overall, our study provides a first general analysis of age-specific selection on mating choosiness. Our main finding is that the relative contribution of each age class to the offspring pool is the key component to understanding the strength of selection on choosiness at each age. This finding has implications for understanding individual variation in mate choice and the evolution of reproductive isolation.

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PEER REVIEW

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OPEN RESEARCH BADGES



This article has earned an Open Materials Badge for making publicly available the components of the research methodology needed to reproduce the reported procedure and analysis. All materials are available at <https://doi.org/10.5061/dryad.hdr7sqvgn>.

DATA AVAILABILITY STATEMENT

The notebook associated with the numerical simulations is available at <https://doi.org/10.5061/dryad.hdr7sqvgn>.

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SUPPORTING INFORMATION

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

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