Which cues are sexy? The evolution of mate preference in sympatric species reveals the contrasted effect of adaptation and speciation.

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Abstract

Mate preferences have a strong effect on adaptation and speciation. In turn, these two evolutionary processes can generate contrasted selective pressures acting on the evolution of preferences. In sympatric species, trait distributions are shaped by similar selective pressures, thus independently promoting similar adaptive traits in different species. When preference targets such adaptive traits, the trait similarity between species may induce heterospecific matings. The evolution of preference for adaptive traits thus likely depends on the ecological interactions between species. Using a mathematical model, we study the evolution of preference towards adaptive *vs.* neutral traits shared by sympatric species. We specifically investigate whether preference for several traits might emerge, despite sensory trade-off. We also test whether preference toward cues linked to adaptation *vs.* species recognition may preferentially evolve. Our mathematical approach reveals the key role of sensory trade-offs and opportunity costs favouring the evolution of preferences targeting adaptive traits rather than traits relevant to species recognition. Our model thus highlights that the evolution of preferences for different traits in sympatric species depends on within-species mating opportunities but also on the niche overlap between species, tuning the heterospecific interactions.

Introduction

The evolution of mate preference plays a major role in the diversification of traits (Chouteau et al., 2017) and species (Stre et al., 1997). Nevertheless, we still know little about the evolutionary factors determining the traits preferentially targeted by preferences, especially the number of cues used during mate choice.

Preferences are based on traits displayed by the parents, but their evolution usually depends on the indirect fitness benefit brought to the offspring carrying locally adapted traits (Neff and Pitcher, 2005). The fitness of the offspring depends not only on the intraspecific competition but also on the ecological interactions with sympatric species. When closely-related species occur in sympatry, sexual interactions with heterospecifics (Gröning and Hochkirch, 2008) can lead to fitness reduction because of limited survival in the resulting hybrids (Merrill et al., 2012), but also because of costly heterospecific courtship and rivalry. These fitness costs generated by heterospecific interactions can promote mate preferences targeting traits that differ between species (McPeek and Gavrilets, 2006; Yamaguchi and Iwasa, 2013). The evolution of preferences may therefore strongly depend on both (1) the selection regimes acting on the targeted traits within species and (2) the distribution of these traits in other species living in sympatry. Such multifactorial selection acting on the different traits displayed by males may then favour the evolution of female preferences targeting several traits. Preference for multiple cues may indeed improve some components of the fitness in the offspring and/or enhance recognition of conspecific males (Candolin, 2003).

By contrast with classical 'magic' traits under disruptive selection (Servedio et al., 2011), natural selection frequently promotes similar traits in different sympatric species (*e.g.* in mimetic species, (Sherratt, 2008)). Indirect fitness benefits enjoyed by the offspring may then induce selection on preference conflicting with species recognition (*e.g.* (Gumm and Gabor, 2005; Higgie and Blows, 2007)). For example, in the spadefoot toad, preference for mating call increases the number of eggs fertilized in choosy females. However, it leads to reproductive interference because of the similarity of calls between sympatric species (Pfennig, 2000). Preferences targeting multiple traits may improve offspring fitness by both transmitting adapted alleles and enhancing species recognition. For example, in field crickets of the genus *Teleogryllus*, female targets both (1) cuticular hydrocarbons, providing fitness benefits to their offspring (Berson and Simmons, 2019), and (2) male calling song (Hill et al., 1972) that differentiates sympatric species (Moran et al., 2020).

While natural and sexual selections may promote preference based on multiple traits (Pomiankowski and Iwasa, 1993; Iwasa and Pomiankowski, 1994), several constraints might limit the number of traits targeted by preference. Preferences are generally associated with fixed costs generated by mate searching, and preference targeting multiple traits might increase these costs. Theoretical studies show that the increased costs of preference based on different traits may promote preference based on the single trait providing the most significant benefit (Schluter and Price, 1993; Pomiankowski and Iwasa, 1993; Iwasa and Pomiankowski, 1994). The number of available partners displaying the preferred combination of traits may also impact the evolution of preference for multiple traits. Opportunity costs associated with rejection of unpreferred males by choosy females may increase, when the number of targeted traits grows.

The evolution of multiple traits preference may also be limited by the complex cognitive processes involved. Multiple traits-based mate choice may thus preferentially evolve in species where multiple sensory systems allow such cognitive integration. Due to evolutionary trade-offs, the development of sensory systems is frequently associated with the regression of others (Barton et al., 1995; Nummela et al., 2013). Moreover, physical constraints may generate sensory trade-offs: for

example, a visual system model of the surfperch reveals a trade-off in the performance between luminance and chromatic detection because of the limited numbers of the different types of cones in the eyes (Cummings, 2004). Neural integration of multiple information may also be limited, generating trade-offs in using multiple traits in decisions. In the swordtail fish *Xiphophorus pygmaeus*, females prefer a visual or an olfactory trait when experimenters expose them to the variation of only one out of the two traits in the potential mates. However, when both traits vary in potential mates, females do not express preference (Crapon de Caprona and Ryan, 1990), suggesting that sensory trade-off limits the use of multiple traits in preference.

These contradictory developmental and ecological factors call for a general framework determining the evolution of preferences towards different traits shared between sympatric species, that may be either neutral or locally adaptive. Here, we use mathematical modelling to investigate the evolution of preference based on multiple traits. We study the evolution of preference towards two evolving traits (T_1 and T_2) shared by two sympatric species (A and B). We aim at identifying how selection regimes acting on the targeted traits, as well as reproductive interference between species, favour (1) preference for locally adapted trait vs. trait enhancing species recognition and 2) single or multiple traits preference.

Results

Model overview

We consider two closely-related species (A and B) living in sympatry and assume that individuals from both species display two traits that could be targeted by female preferences. We assume that both traits are controlled by independent haploid loci (called T_1 and T_2, respectively), with two possible alleles 0 or 1 at each locus. We fix the genotypic distribution in species B by assuming that all individuals carry the allele 1 at both trait loci. The loci P_1 and P_2 then determine the value of traits T_1 and T_2 respectively preferred by females. Female preference can target either or both traits (1 and 2) displayed by the males: a preference locus M controls the relative level of attention paid by the female toward trait 1 *vs.* trait 2 expressed by males. We thus introduced γ as the preference direction modulating the level of attention on either trait (Figure 1). We assume that a resident and a mutant alleles can occur at locus M with different values of γ (γ_r and γ_m). We then study the evolution of preference direction in focal species A. Assuming non-overlapping generations and relying on an adaptive dynamics framework, we investigate the fixation of new mutant alleles and estimate the equilibrium preference direction (γ^*). We note γ_{t_0} the ancestral preference direction.

The evolution of the preference direction depends on the survival of the produced offspring. We thus assume that the traits T_1 and T_2 displayed by the individuals can modify their survival. We note s_1 and s_2 the selective advantages associated with allele 1 at locus T_1 and T_2, respectively. We assume that $s_1 \geq 0$ and $s_2 \geq 0$, so that natural selection acting within species A promotes similarity with species B (because allele 1 is fixed for both traits in species B). We also assume that females can encounter and have sexual interactions with heterospecifics. Such sexual interactions lead to fitness costs but do not produce any viable offspring.

We also assume that the level of attention on one trait diminishes the attention on the alternative one. We investigate several shapes of this trade-off tuned by the parameter a (Figure 1). Finally, we assume that females refusing a mating opportunity may eventually fail to reproduce with a probability c, leading to a cost of choosiness. We investigate how the cognitive trade-off and the

costs of choosiness impact the evolution of the direction of preference, that might lead to preference for either a single or multiple traits.

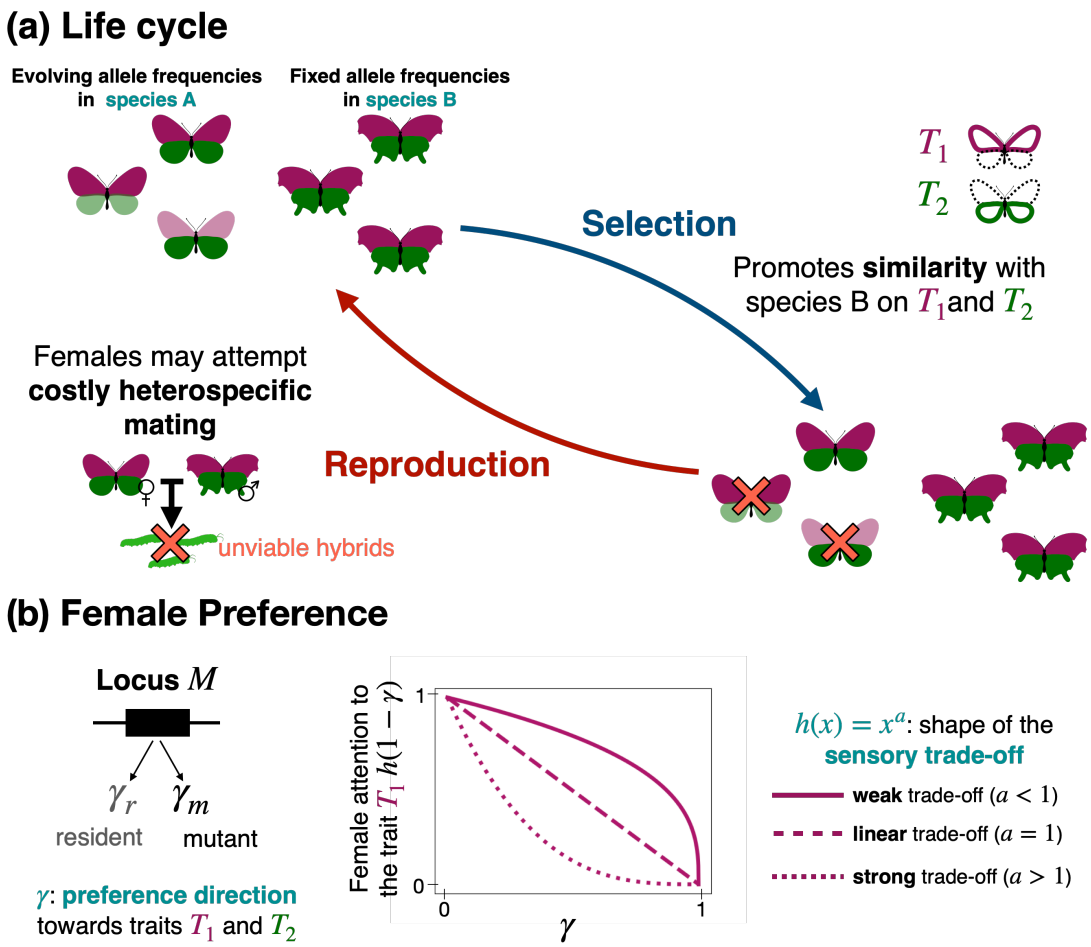

Figure 1: **Schematic description of the model.** (a) **Life cycle. The evolution of the preference may depend on the interactions between species and on the natural selection acting on the preferred traits. Here, we assume two sympatric species A and B, depicted in this scheme as butterfly species with different wing shapes. The individuals can display two traits T_1 and T_2, represented by the forewing and hindwing colours as an example. We study the coevolution of the trait values (0 or 1, shown as intense *vs.* light color of the wings) and the preference in species A. We assume that all individuals in species B displayed the trait value 1 (intense color) at both traits. We assume a selection step, promoting trait value 1 at both traits in species A, therefore increasing similarity with species B, where value 1 is fixed for both traits. We then assume a reproduction step, where the mating success of the different individuals in species A depends on the traits and preferences carried by males and females. In particular, females of species A may attempt costly and unfertile sexual interactions with males of species B depending on their preferences. (b) Genetic basis of preference. Depending on the genotype at locus M, females modulate their level of attention towards either trait displayed by males (preference direction γ). We also assume that the level of attention on one trait diminishes the attention on the alternative one. We investigate several shapes of this trade-off tuned by the parameter a.**

'Good genes' *vs.* reinforcement

To explore the evolution of preference enhancing offspring fitness *vs.* species recognition, we computed the equilibrium value of the preference direction γ^* when assuming that natural selection acts on trait T_1, increasing similarity with species B, while the trait T_2 is neutral. We investigate different strengths of natural selection acting on trait T_1 (s_1) and reproductive interference (c_{RI}) (Figure 2).

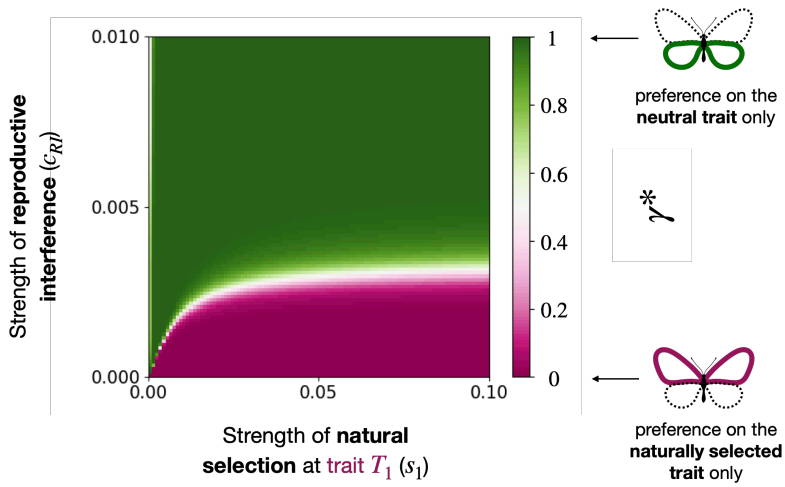

Figure 2: **Evolution of female preference (γ^*) towards traits (T_1 and T_2) displayed by males, depending on the strength of natural selection acting on trait T_1 (s_1) and the strength of reproductive interference (c_{RI}) when T_2 is neutral ($s_2 = 0$).**

To disentangle the relative effects of the contrasted selection pressures acting on the evolution of preference, we also define the selection coefficients S_{os}, S_{or}, S_{ri} and S_c reflecting the effect of offspring survival, reproductive success, reproductive interference and opportunity costs respectively (see expression in Equations (A21), (A22), (A16) and (A18)), by rewriting the change of mutant frequency P_M at locus M (given in Equation (A10))

$$\Delta P_M = P_M(1 - P_M)\delta\gamma\,(S_{ns} + S_{ss} + S_{ri} + S_c)\,, \tag{1}$$

where $\delta\gamma = \gamma_m - \gamma_r$ is the effect of the mutant allele on the preference direction. When a selection coefficient is positive (resp. negative), selection promotes the evolution of preference towards the trait under selection T_2 (reps. the trait under selection T_1) (Figure 3).

The neutral trait becomes a reliable cue for species recognition

Figure 2 indicates that reproductive interference between species A and B promotes the evolution of preference targeting the neutral trait T_2. A female of species A prefers trait value 0 (Figure A1), reducing sexual interaction with males from species B always displaying the trait value 1 (see Equation (A6). Sexual selection thus increases the phenotypic divergence with heterospecific (see

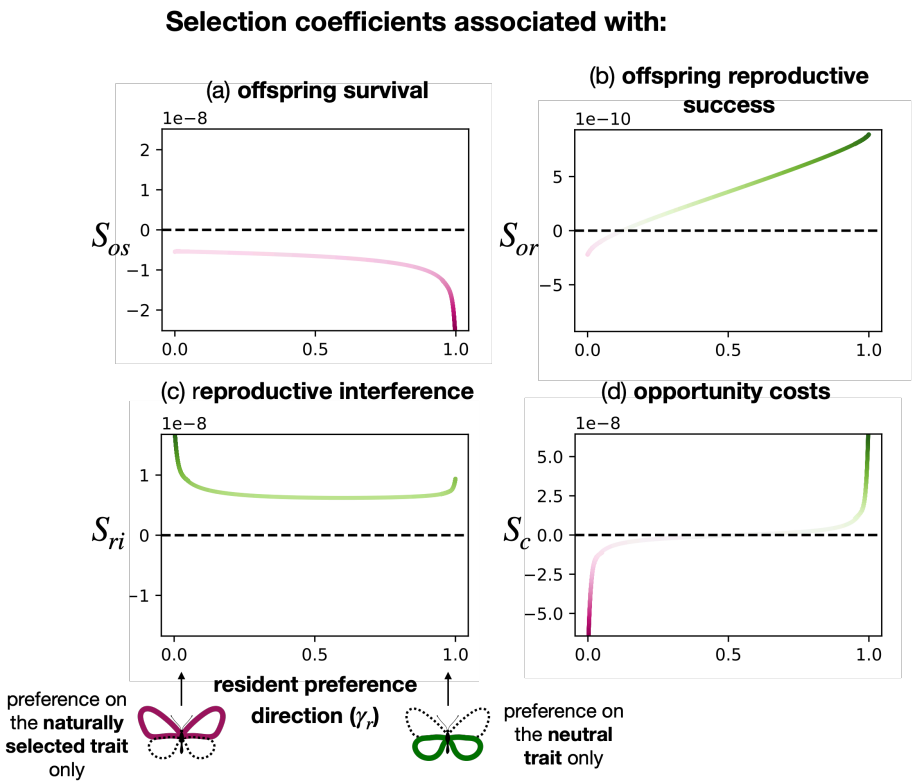

Figure 3: **Selection coefficients associated with (a) offspring survival (S_{os}), (b) offspring reproductive success (S_{or}), (c) reproductive interference (S_{ri}) and (d) opportunity costs (S_c), depending on the resident preference direction (γ_r).** We fixed the level of reproductive interference ($c_{RI} = 0.0025$) and assume that trait T_1 is under natural selection ($s_1 = 0.02$) while trait T_2 is neutral ($s_2 = 0$). When the line is green (reps. purple) the corresponding evolutionary force (offspring survival, offspring reproductive success, reproductive interference and opportunity costs) promotes the evolution of preference towards the neutral selection T_2 (reps. the trait under selection T_1). The more intense the color the more intense the selection.

Equation (A1)), making the neutral trait T_2 a more reliable cue for species recognition in species A.

Figure 3(c) confirms that the selective advantage owing to reproductive interference rises when the resident preference tends to target the neutral trait. When preference towards the neutral trait T_2 increases, the stronger sexual selection enhances the phenotypic divergence with heterospecific (Figure A2), making T_2 a more reliable cue for species recognition. Then in a adaptive dynamic framework, during the recurrent fixation of mutant allele, a positive feedback loop promotes preference towards the neutral trait T_2.

Species interaction limits preference enhancing offspring fitness

Figure 2 also indicates that natural selection promotes preference towards the trait under selection T_1. Females from species A thus tend to prefer males with the allele 1 at the trait under selection (Figure A1), also displayed by the males of the sympatric species B. However, when there is reproductive interference between species, preference should be more likely to target traits enhancing species recognition than offspring fitness, but this might depend on the relative strength of natural selection on the trait *vs.* selection generated by reproductive interference.

Figure 3(a) reveals that the selective benefit of producing adapted offspring decreases when resident preference targets the trait under selection. When preference towards the trait under selection T_1 increases, the stronger sexual selection reduces the genetic diversity (Figure A2). As most males displayed the well-adapted trait value 1 (Figure A2), the advantage of preference towards the trait under selection therefore decreases. By contrast with the evolution of the preference towards the neutral trait, a negative feedback loop limits the evolution of preference towards the trait under selection.

Moreover, the selective benefit of producing sexy sons promotes preference towards the neutral trait (Figures 3(b) and A3). Because natural selection strongly reduces the phenotypic diversity at trait T_1, almost all males display the sexy trait value at T_1 (Figure A2). By contrast, males exhibiting the trait value 0 at the neutral trait T_2 benefit from a sexual selection advantage, as compared to other males. Female preference towards males exhibiting this trait values at trait T_2 is then further advantaged through an indirect benefit gained by their sexier sons (see Equation (A19)). The 'sexy son' advantage persists as long as the strength of reproductive interference is sufficiently high and promotes preference for the trait value 0 at the neutral trait T_2 (Figure A3). This enhanced 'sexy son' advantage associated with female preference toward neutral as compared to adaptive traits can explain why preference toward cues improving species recognition rather can preferentially evolved.

Evolution of multiple traits preference enhancing both offspring fitness and species recognition

Nevertheless, the contrasted selective pressures may promote the evolution of preference towards both traits, therefore jointly enhancing offspring fitness and species recognition. We thus test which values of opportunity costs (c) and shapes of the trade-off function h (through the parameter a) allow the evolution of multiple trait preference.

Low opportunity costs and weak sensory trade-off allow the evolution of multiple trait preference

Figure 4(a) shows that a weak cognitive trade-off ($\log(a) < 0$) and low opportunity costs (c) allow the evolution of multiple trait preference. This preference enhances offspring fitness and species recognition by using the trait under selection and the neutral trait, respectively. More substantial cognitive trade-offs or opportunity costs prevent the evolution of such multiple traits preference. Interestingly, a linear trade-off ($\log(a) = 0$) leads to preference based on a single trait. A concave trade-off ($a < 1$) is thus necessary for the evolution of multiple trait preference.

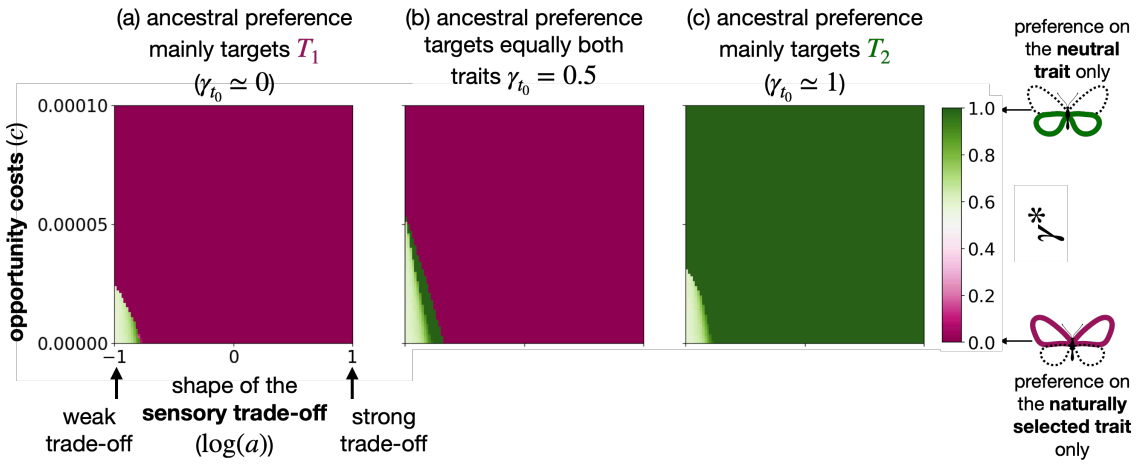

Figure 4: **Evolution of female preference towards a trait under selection T_1 and a neutral trait T_2 displayed by males (γ^*) depending on the shape of the cognitive trade-off function (through the parameter a) and the cost of choosiness c for different ancestral preferences**. We assume ancestral preference targeting: (a) mainly trait T_1 ($\gamma_{t_0} = 0.01$), (b) equally both traits ($\gamma_{t_0} = 0.5$), (c) mainly trait T_2 ($\gamma_{t_0} = 0.99$). We assume reproductive interference ($c_{RI} = 0.025$), that trait T_1 is under natural selection ($s_1 = 0.02$) and trait T_2 is neutral ($s_2 = 0$).

Ancestral single trait preference can limit the evolution of multiple trait preference

We then investigate the effect of ancestral preferences on the evolution of preference direction expressed in females. We compare ancestral preferences targeting: equally both traits ($\gamma_{t_0} = 0.5$), mainly the trait under selection or neutral trait ($\gamma_{t_0} = 0.01$ or $\gamma_{t_0} = 0.99$).

Figures 4(a), 4(b) and 4(c) show that preferences are biased towards ancestral preference. Ancestral single trait preference thus reduces the parameter space where multiple trait preference evolves. Interestingly, ancestral preference influences the evolution of mate preference when substantial trade-offs and opportunity costs are assumed. Under a strong trade-off, preference based on both traits effectively leads to poor attention towards both traits. This lack of attention towards both cues therefore creates a fitness valley preventing the switch of female attention from one trait to the alternative one. When the female choice is ancestrally mainly based on one trait, positive selection promoting choice for the alternative trait may not be powerful enough to cross this fitness valley.

Figure 3(d) indicates that opportunity costs also favour the evolution of preference towards the ancestrally most preferred trait because this trait is then likely to be highly prevalent in the males suitable for reproduction. Mate choices mainly based on the already preferred trait then benefit from reduced opportunity costs (see Equation (A17)).

Moreover, when the ancestral preference mostly target one trait, figure 3(b) indicates that sexual selection promotes preference for this trait. When a trait is already sexy, females carrying a mutant allele increasing their attention on this trait are likely to produce more sexy sons.

These mechanisms explain why the evolution of preference strongly depends on the ancestral

traits, as observed in figure 4. Interestingly, figure 4(b) also shows that when the ancestral preference equally targets both traits, preference targeting the trait under selection is favoured. However, this may depend on the strength the sensory trade-off and on the opportunity costs.

From multi-trait preference to preference targeting the adaptive trait only

When ancestral preference equally targets both traits, strong sensory trade-off promotes preference towards adaptive traits (Figure 4). When assuming a large sensory trade-off ($a > 1$), the ancestral preference leads to poor attention towards both traits. This poor attention toward male traits then limits the previously described 'sexy sons' effect that promotes preference towards the neutral trait (Figure A4).

Large opportunity costs also promote single-trait preference targeting the trait under natural selection T_1, when assuming that ancestral preference equally targets both traits. Indeed natural selection acting on trait T_1 reduces phenotypic diversity in species A and, therefore, reduces opportunity costs associated with preference based on the trait T_1 in this species (see Equation (A17) and Figure A5).

In contrast, intermediate opportunity costs allow the evolution of multiple traits preferences with biased attention towards the neutral trait T_2 (Figure 4). When opportunity cost are not too high, the 'sexy son' advantage obtained through slighty biased attention toward the neutral trait balances the opportunity costs. However, the preference for the adaptive trait become more advantageous when opportunity costs further increase : such preference alleviates opportunity costs, thus favouring the single trait preference targeting the trait T_1 when opportunity costs becomes too large.

Connecting 'good genes' with reinforcement

To explore the impact of natural selection acting on mating cues shared with other sympatric species on the evolution of female preferences, we computed the equilibrium value of the preference direction γ^* for different strengths of (1) natural selection at trait T_1 and T_2 (s_1 and s_2) and of (2) levels of reproductive interference (c_{RI}).

Without species interactions, the trait under stronger selection is sexy

As expected, Figure 5(a) shows that without species interactions ($c_{RI} = 0$), female preference mainly targets the trait under stronger selection. Furthermore, figure 5(a) also highlights that in the absence of reproductive interference, multiple trait preference is likely to emerge when both traits are under strong selection.

Assuming reproductive interference, the trait under lower selection becomes sexy

By contrast, assuming reproductive interference with species B ($c_{RI} > 0$), females from species A mainly target a single trait. Surprisingly, females generally tend to focus on the trait with the lowest impact on fitness (figures 5(b) and 5(c)).

Altogether our results shows the relevance of jointly considering the effect of natural selection acting on mating cues within species, but also on the cues displayed in closely-related species living in sympatry to understand the evolution of mate choice.

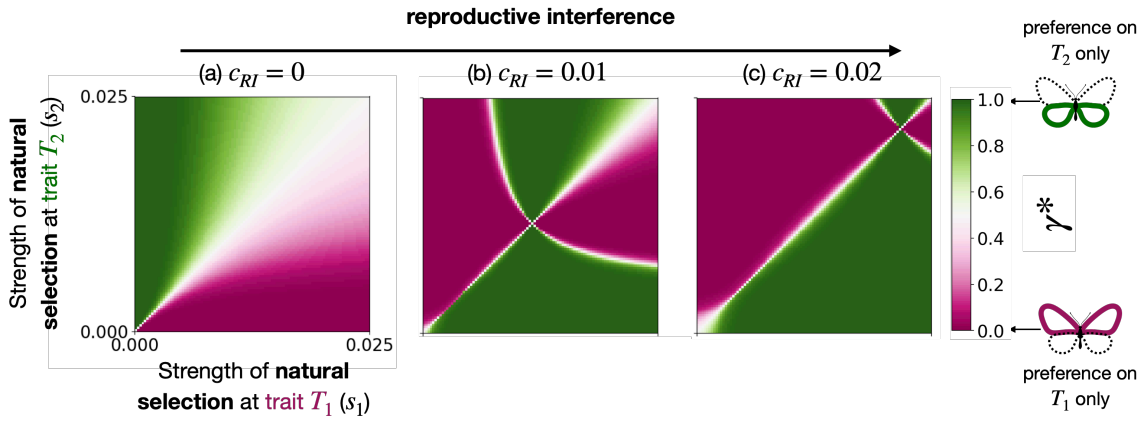

Figure 5: **Evolution of female preference towards traits (T_1 and T_2) displayed by males (γ^*), depending on the strength of natural selections acting on trait T_1 and T_2 (s_1 and s_2), for different strengths of reproductive interference (c_{RI}).** We assume (a) $c_{RI} = 0$, (b) $c_{RI} = 0.01$ and (c) $c_{RI} = 0.02$.

Discussion

Evolutionary biologists have extensively studied the evolution of mate preferences in the light of the 'good genes' hypothesis (Puurtinen et al., 2009) or the context of reinforcement (Servedio and Noor, 2003). By jointly considering (1) the selection regimes acting on the targeted traits within species, as well as (2) interactions with other species living in sympatry, our theoretical study provides a general framework reconciling these research fields.

We focused on natural selection regimes shared between sympatric species promoting species similarity and increasing risks of reproductive interference. Our approach drastically differs from classical studies on reinforcement, focusing on 'magic traits', submitted to disruptive selection between species (Servedio et al., 2011). Because 'magic traits' are honest signals of both local adaptation and species identity, antagonistic selection regimes are not involved in the evolution of mate preferences in such framework. Here, we specifically investigate conflicting selections acting on the evolution of mate preferences, and explore the emergence of single vs. multiple trait preference.

Our results show that conflicting selection may promote the evolution of multiple trait preference. Nevertheless, opportunity costs limits the evolution of such preference and can change the trait mainly targeted by female choice. The opportunity costs promote preference based on naturally selected traits rather than traits allowing species recognition. As natural selection erodes phenotypic diversity, preference based on traits allowing species recognition leads to stronger opportunity cost, promoting preference targeting the naturally selected traits. However when opportunity costs are more limited, our model highlights that female preference may then preferentially target traits that differ from other species. For example, in *Heliconius* butterflies, where females are usually mated rapidly after emergence because of the high density of suitable males, female preference have been shown to target chemical cues differentiating sympatric species (González-Rojas et al., 2020).

In our model, species recognition traits are assumed neutral. However, selective constraints may

also act on traits used as species recognition cues. For instance, variation in such cues may influence their detection probability by predators: the conspicuousness of a trait may enhance the identification by sexual partners but may in turn also increase parasitism and predation risks (observed on visual, acoustic and olfactory cues in numerous organisms reviewed in Zuk and Kolluru (1998)). Increasing costs of sexual trait conspicuousness may theoretically promote the display of combinations of cryptic traits allowing recognition (Johnstone, 1995), therefore promoting preference towards multiple cues.

Our results also highlight how indirect fitness benefit and/or reproductive interference can promote female preference for multiple traits. The evolution to such a preference occurs only when the cognitive trade-off is weak. Therefore, multiple traits preference is more likely to emerge in species where complex neural processes occur. Nevertheless, several alternative decision mechanisms may reduce this cognitive trade-off. For example, sequential/hierarchical mate preference, whereby targeted traits are processed in a hierarchical order, efficiently produces a decision, even considering many traits (Gigerenzer et al., 1999). Sequential mate preference is common (*e.g.* (Shine and Mason, 2001; Eddy et al., 2012; Gray, 2022)) and may allow the evolution of multiple traits preference. Sequential mate choice may emerge because some traits are visible at long distances (such as colour or calls), whereas others are perceived only at short distances (such as oviposition site guarded by males or male-emitted pheromones) (*e.g.* (Candolin and Reynolds, 2001; López and Martín, 2001; Mérot et al., 2015)).

The distance at which choosers perceive different traits may play a key role in reproductive isolation (Moran et al., 2020). Females attracted by a trait of the heterospecific males detected at a long distance may have already spent time and energy or need to deploy substantial efforts to avoid heterospecific mating. Therefore, females may still suffer from increased costs associated with reproductive interference, even if they eventually manage to avoid mating with heterospecific males (Gröning and Hochkirch, 2008). Hence reproductive interference may promote preference targeting traits detected from far distances that efficiently reduce heterospecific interactions.

Reproductive isolation between species also depends on the niche of individuals of both species. Mating may preferentially occurs between individuals sharing the same niche leading to niche-based assortative mating. Niche segregation may play a key role in the evolution of reproductive isolation. In two treefrog species, differing by their mating call (Park et al., 2013), different spatial and temporal segregations in calling and resting places during the breeding period increase reproductive isolation (Borzée et al., 2016). As well as sequential mate preference, niche segregation may efficiently participate in reproductive isolation without generating trade-off with a preference for other traits.

Our study shows how natural and sexual selections may have a conflicting influence on the evolution of mate choice, and specifically on the emergence of multiple traits preference in sympatric species. Our study highlights the importance of (1) identifying the trade-off limiting attention towards different traits and of (2) estimating the strength of opportunity costs to understand what traits are likely to be targeted by preference.

Method

Selection regime acting on the displayed traits

We assume that the traits T_1 and T_2 displayed by the individuals can modify their survival. We define f_i and f_i' as the frequencies of genotype $i \in \{1, 2\}$ in the focal species before and after a step

of natural selection acting on survival, respectively. The resulting frequency after selection, f_i' is then given by

$$f_i' = \frac{w_i}{\overline{w}} f_i, \tag{2}$$

where w_i is the fitness component due to natural selection of an individual of genotype i, while $\overline{w}$ is the average fitness component due to natural selection averaged.

$$\overline{w} = \sum_{i \in \mathcal{G}} w_i f_i, \tag{3}$$

where $\mathcal{G}$ is the set of all genotypes.

We note s_1 and s_2 the selective advantages associated with allele 1 at locus T_1 and T_2, respectively. When natural selection favours individuals with allele 0 at locus T_i, s_i is negative for $i \in \{1, 2\}$.

The fitness component due to natural selection of an individual of genotype i is thus given by:

$$w_i = (1 + (T_1)_i s_1)\,(1 + (T_2)_i s_2)\,, \tag{4}$$

where $(T_j)_i$ is the value of trait T_j (0 or 1) of individuals of genotype i for $j \in \{1, 2\}$.

Reproductive success depending on female preference on traits displayed by males

Females generally use both traits in preference but may vary in their relative attention given to trait 2 *vs.* trait 1. This relative attention depends on the preference direction parameter γ. Alleles at locus M determine the preference direction: allele 0 (resp. 1) is associated with the value γ_r (resp. γ_m). The preference direction of a female of genotype j is thus given by:

$$\gamma_j = (1 - (M)_j)\gamma_r + (M)_j \gamma_m, \tag{5}$$

where $(M)_j$ is the allele (0 or 1) at locus M in genotype j. We assume that a cognitive trade-off, described by the function h, also impacts the relative attention to the two traits. $h(1-\gamma)$ and $h(\gamma)$ determine the attention on trait 1 and 2 where $a \in [0, +\infty)$ and

$$h(x) = x^a, \forall x \in [0, 1].$$

The function h is non-decreasing, so that attention on one trait diminishes attention on the alternative one. Moreover, $h(0) = 0$ and $h(1) = 1$, so in the two extreme cases, the female choice relies on a single trait. The parameter a tunes the shape of the trade-off function h (Figure 1):

- when $a = 1$, h is linear, leading to a **linear trade-off**, where the female attention on traits 1 (resp. 2) is proportional to $1 - \gamma$ (resp. γ).
- when $a < 1$, h is concave, leading to a **weak trade-off** between attention towards the two male traits. Females can thus use both traits for mate choice.
- when $a > 1$, h is convex leading to a **strong trade-off** in female attention between the two traits. Females focusing on one trait largely ignore the alternative trait, and intermediate values of γ lead to poor attention to both traits.

Therefore, when a female of genotype j in species A encounters a male of genotype k, she accepts the male with probability

$$\phi(j,k) = \Big(1 - \mathbb{1}_{(P_1)_j \neq (T_1)_k} \rho h (1-\gamma_j)\Big)\Big(1 - \mathbb{1}_{(P_2)_j \neq (T_2)_k} \rho h (\gamma_j)\Big), \tag{6}$$

where $\mathbb{1}_{\{.\}}$ is the indicator function that returns 1 if the condition in the subscript is realized and 0 otherwise. The mating probability of a couple depends on the match between the female's preferred traits and the male's traits values. The parameter ρ quantifies the strength of female preference.

During an encounter between individuals from different sexes, $T(j)$ gives the probability that a female of genotype j accepts a conspecific male (Otto et al., 2008):

$$T(j) = \sum_{k \in \mathcal{G}} \overbrace{\frac{N}{N+\tilde{N}} f'_k}^{\substack{\text{probability of encountering} \\ \text{a conspecific male} \\ \text{of genotype } k}} \overbrace{\phi(j,k)}^{\substack{\text{probability of accepting} \\ \text{a conspecific male} \\ \text{of genotype } k}}, \tag{7}$$

where N and $\tilde{N}$ are the densities of species A and B, respectively.

A female of genotype j may also accept a heterospecific male with a probability

$$T_{RI}(j) = \sum_{k \in \mathcal{G}} \overbrace{\frac{\tilde{N}}{N+\tilde{N}} \tilde{f}_k}^{\substack{\text{probability of encountering} \\ \text{an heterospecific male} \\ \text{of genotype } k}} \overbrace{c_{RI}\phi(j,k)}^{\substack{\text{probability of accepting} \\ \text{an heterospecific male} \\ \text{of genotype } k}}, \tag{8}$$

where $c_{RI} \in [0,1]$ captures the investment of females in interspecific mating. We assume that heterospecific crosses never produce viable offspring and that a female engaged in such matings cannot recover the associated fitness loss.

Knowing that a female of genotype j has mated with a conspecific male, the probability that this male is of genotype k is given by

$$\Phi(j,k) = \frac{\phi(j,k) f'_k}{\sum_{l \in \mathcal{G}} \phi(j,l) f'_l}. \tag{9}$$

If females only encountered one male, the probability of crosses between a female of genotype j and a conspecific male of genotype k would be

$$\mathcal{P}^1(j,k) = f'_j T(j) \Phi(j,k). \tag{10}$$

However, we assume that females refusing a mating opportunity can encounter another male with a probability $1-c$. We interpret c as the cost of choosiness (similar to the coefficient c_r, referred to as relative cost of choosiness in (Otto et al., 2008)). The probability of crosses between a female of genotype j and a conspecific male of genotype k is thus given by

$$\begin{aligned} \mathcal{P}(j,k) &= \sum_{n=0}^{+\infty} \left((1 - T(j) - T_{RI}(j))\,(1-c)\right)^n \mathcal{P}^1(j,k) \\ &= \frac{\mathcal{P}^1(j,k)}{c + (1-c)(T(j) + T_{RI}(j))}, \end{aligned} \tag{11}$$

where $((1 - T(j) - T_{RI}(j))\,(1 - c))^n$ is the probability that a female of genotype j rejects the n males she first encounters and then encounters an $(n + 1) - th$ male.

The contribution to the next generation of a mating between a female of genotype j and a male of genotype k is thus given by

$$m_{j,k} = \frac{T(j)}{c + (1 - c)(T(j) + T_{RI}(j))} \frac{\phi(j, k)}{\sum_l f'_l \phi(j, l)}. \tag{12}$$

Genotypic frequencies after reproduction in the focal species then depend on the contribution to the next generation of the different crosses between females and males of genotype j and k respectively, described by $m_{j,k}$, for all j and k in $\mathcal{G}$. We note $\overline{m}$ the mean value of this contribution across all mating pairs

$$\overline{m} = \sum_{j,k \in \mathcal{G}} f'_j f'_k m_{j,k}. \tag{13}$$

The frequency after reproduction of genotype i in species A is then given by

$$f''_i = \sum_{j,k \in \mathcal{G}} f'_j f'_k \frac{m_{j,k}}{\overline{m}} \beta(i, j, k), \tag{14}$$

where $\beta(i, j, k)$ describes the segregation of alleles during reproduction and provides the probability that a mating between a female of genotype j and a male of genotype k produces an offspring of genotype i. We assume recombination between female and male haplotypes. The offspring inherits any of the two recombined haplotypes with a probability one half.

Mutation

We assume that mutations occur at loci T_1, T_2, P_1 and P_2 within offspring with probability u_{T_1}, u_{T_2}, u_{P_1} and u_{P_2} respectively.

We summarise all the model's variables and parameters in Table A1.

Model exploration

Using QLE analysis to determine the continuously stable preference direction

We perform a Quasi-Linkage Equilibrium (QLE) analysis to estimate the allele frequency change at each locus. QLE analysis assumes that selection is weak and recombination is strong compared to selection. In line with this hypothesis, we assume that s_1, s_2, ρ, c_{RI}, c are of order ε with ε low and that the recombination rates are of order 1. We also assume that mutation rates are of order ε. We perform the QLE analysis using Wolfram Mathematica 12.0, and we present all the details of the analytical results in Appendix A1.

In an adaptive dynamics framework, we use the QLE analysis to estimate the different types of singular preference directions numerically (Rousset, 2004; Geritz et al., 1998):

- Continuously stable preference direction: value of γ convergence stable and uninvaidable.
- Evolutionary repeller: value of γ not convergence stable.

- Branching point: values of γ convergence stable and invaidable (never observed in this study).

We look at the equilibrium preference direction (γ^*) *i.e.* the continuously stable preference direction reached by the dynamics that may depend on ancestral preference (γ_{t_0}). By default we assume that ancestral preference equally targets both traits ($\gamma_{t_0} = 1/2$).

Default parameters

If not specified we use the following parameter values: $\gamma_{t_0} = 1/2$, $P^0_{T_1} = P^0_{T_2} = P^0_{P_1} = P^0_{P_2} = 0.5$, $\tilde{P}_{T_1} = \tilde{P}_{T_2} = 1$, $s_1 = s_2 = 0$, $\rho = 0.01$, $c = 0$, $c_{RI} = 0$, $a = e^{-1}$, $N = \tilde{N} = 10$, $u_{T_1} = u_{T_2} = 0.002$, $u_{P_1} = u_{P_2} = 0.00002$.

Scripts availability

Scripts are available online at github.com/Ludovic-Maisonneuve/evolution_of_multiple_traits_preference.

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Appendix

A1 QLE analysis

Evolution of mating traits under natural and sexual selection

First, we explored the relative effects of natural and sexual selections on the evolution of traits in species A. Following the QLE approach, the change of allele 1 frequency at T_i, for $i \in \{1, 2\}$, after one generation in this species is given by:

$$\Delta P_{T_i} = G_{T_i} \overbrace{\left(s_i + \overline{\rho}_i \left(P_{P_i} - \frac{1}{2}\right)\right)}^{\text{natural and sexual selections}} \overbrace{-2u_{T_i}(P_{T_i} - 1/2)}^{\text{action of mutations}} + O(\varepsilon^2), \tag{A1}$$

where G_I is the genetic diversity at locus $I \in \{T_1, T_2, P_1, P_2, M\}$ given by

$$G_I = P_I(1 - P_I), \tag{A2}$$

and $\overline{\rho}_1$ and $\overline{\rho}_2$ are the average strengths of preference on traits T_1 and T_2 respectively in the population

$$\overline{\rho}_1 = \rho\left((1 - P_M)h(1 - \gamma_r) + P_M h(1 - \gamma_m)\right), \tag{A3}$$

$$\overline{\rho}_2 = \rho\left((1 - P_M)h(\gamma_r) + P_M h(\gamma_m)\right). \tag{A4}$$

While the action of natural selection simply depends on the advantage of trait value 1 due to natural selection s_i, the effect of sexual selection is modulated by the average strength of preference on trait T_i in the population ($\overline{\rho}_i$). Sexual selection promotes the allele 1 when most females prefer the associated trait value 1 *i.e.* when $P_{P_i} > 1/2$.

Evolution of a mutant modifying preference direction

Now we explore the selection acting on preference loci P_1 and P_2, determining which trait value is sexy at traits T_1 and T_2. Following the QLE approach, the change of allele 1 frequency at P_i, for $i \in \{1, 2\}$, after one generation in this species is given by:

$$\Delta P_{P_i} = \Delta^{\text{dir-RI}} P_{P_i} + \Delta^{\text{dir-c}} P_{P_i} + \Delta^{\text{ind}} P_{P_i} - 2u_{P_i}(P_{P_i} - 1/2), \tag{A5}$$

where $\Delta^{\text{dir-RI}} P_{P_i}$, $\Delta^{\text{dir-c}} P_{P_i}$, $\Delta^{\text{ind}} P_{P_i}$ and $-2u_{P_i}(P_{P_i} - 1/2)$ describes the effect of direct selection due to reproductive interference and opportunity costs, indirect selection and mutations.

Reproductive interference promotes preference for the trait value that is more common within conspecific than within heterospecific.

The effect of reproductive interference on the change of allele 1 frequency at P_i, for $i \in \{1, 2\}$ is given by

$$\Delta^{\text{dir-RI}} P_{P_i} = G_{P_i} \overline{\rho}_i c_{RI} \frac{\tilde{N}}{N} (P_{T_i} - \tilde{P}_{T_i}), \tag{A6}$$

where $\tilde{P}_{T_i}$ is the frequency of allele 1 at locus T_i in species B.

Selection acting on locus P_i depends on how much preference targets the trait T_i, captured by $\overline{\rho}_i c_{RI}$. Reproductive interference promotes preference for the trait value 1 when trait value 1 is more common within conspecific than within heterospecific *i.e.* $P_{T_i} - \tilde{P}_{T_i}$.

As expected, the effect of reproductive interference mainly depends on the density ratio between species B and A, $\tilde{N}/N$: the probability that a female in species A encounters an heterospecific male increases with $\tilde{N}/N$. Selection caused by reproductive interference also increases with the strength of preference ρ. Strong preference leads to more significant fitness differences between females, with different preferences intensifying selection due to reproductive interference.

Sympatry with other species intensifies opportunity costs

Preference allows the rejection of heterospecific males but also leads to the rejection of conspecific males. After rejecting a male, a female has a probability c of not encountering another male leading to an opportunity cost. The effect of these costs on the change of allele 1 frequency at P_i, for $i \in \{1, 2\}$ is given by

$$\Delta^{\text{dir-c}} P_{P_i} = G_{P_i} \overline{\rho}_i c \frac{N + \tilde{N}}{N} (P_{T_i} - 1/2). \tag{A7}$$

Opportunity costs disfavour preference for trait value 1 when this trait value is the scarcest in the population *i.e.* $P_{T_i} < 1/2$. Surprisingly, selection due to opportunity costs increases with the proportion of heterospecifics. When a female rejects a conspecific male, she must wait to encounter another suitable male. However, females will be likely to encounter heterospecific males before encountering a conspecific male, making the rejection of a conspecific more dramatic when conspecific males are rare. The effect of opportunity costs is thus proportional to the average number of males a female will encounter until she encounters a conspecific $(N + \tilde{N})/N$.

Indirect selection promotes preference producing locally adapted offspring and sexy sons

Frequencies at preference loci P_1 and P_2 not only directly change the fitness because this modify reproductive interference and opportunity costs but also because of associations with different alleles at the traits loci T_1 and T_2 in the offspring, leading to contrasted indirect fitness benefits. Within offspring, the preference allele at locus P_i becomes associated with the preferred alleles at trait T_i for $i \in \{1, 2\}$. Under the QLE assumptions, the genetic association between alleles 1 at loci T_i and P_i, for $i \in \{1, 2\}$, is given by

$$D_{T_i P_i} = \overline{\rho}_i G_{T_i} G_{P_i}. \tag{A8}$$

Because of mate preference, there is a positive association between the genetic basis of preference for one trait value and the genetic basis of this trait value.

The term describing the effect of indirect selection on the change of allele 1 frequency at P_i, for $i \in \{1, 2\}$ is given by

$$\Delta^{\text{ind}} P_{P_i} = D_{T_i P_i} \left(s_i + \overline{\rho}_i \left(P_{P_i} - \frac{1}{2} \right) \right). \tag{A9}$$

When the mutant is associated with a trait value, direct selection on this trait indirectly affects the change of mutant frequency. Then indirect selection promotes the evolution of preference towards trait value promoted by natural or sexual selection.

Evolution of a mutant modifying preference direction

We investigate the evolution of the focus of female preference on either trait. We thus study the invasion of a mutant at locus M associated with the value γ_m, differing from the value γ_r associated with the ancestral allele. Under the QLE approximation, the allele frequency variation at the preference locus can be divided into three terms, denoted $\Delta^{\text{dir-RI}}, \Delta^{\text{dir-c}}$ and $\Delta^{\text{ind}} P_M$, reflecting the effect of direct selection due to reproductive interference and opportunity costs and indirect selection, on the change of the mutant frequency ΔP_M respectively.

$$\Delta P_M = \Delta^{\text{dir-RI}} P_M + \Delta^{\text{dir-c}} P_M + \Delta^{\text{ind}} P_M + O(\varepsilon^3). \tag{A10}$$

Reproductive interference promotes preference targeting the trait leading to strongest species recognition.

The effect of reproductive interference on the change of mutant frequency is given by

$$\Delta^{\text{dir-RI}} P_M = G_M c_{RI} \frac{\tilde{N}}{N} \Bigg(\delta\rho_1 \left(P_{P_1} - \frac{1}{2} \right) \left(P_{T_1} - \tilde{P}_{T_1} \right) + \delta\rho_2 \left(P_{P_2} - \frac{1}{2} \right) \left(P_{T_2} - \tilde{P}_{T_2} \right) \Bigg), \tag{A11}$$

where $\delta\rho_1$ and $\delta\rho_2$ quantify the effect of the mutant allele on the preference for trait T_1 and T_2, respectively, compared to the resident allele:

$$\delta\rho_1 = \rho \left(h(1-\gamma_m) - h(1-\gamma_r) \right), \tag{A12}$$

$$\delta\rho_2 = \rho \left(h(\gamma_m) - h(\gamma_r) \right). \tag{A13}$$

For instance, when $\delta\rho_2 > 0$, the mutant allele leads to more attention on trait T_2 than the resident allele. Note that h is an increasing function: $\delta\rho_1$ and $\delta\rho_2$ thus have opposite signs, *i.e.* when mutant allele increases female attention on one trait, it also decreases female attention on the other trait.

Reproductive interference promotes preference for the trait allowing more accurate species recognition. Selection due to reproductive interference depends on relative phenotypic frequencies in both species. Preference for a trait leads to increased intraspecific matings than expected under random mating when the targeted trait is more common within species A than within species B. The higher the difference in trait frequencies between species, the more substantial species recognition is.

Because we have

$$\delta\rho_1 \approx -\delta\gamma\rho h'(1-\gamma_r), \tag{A14}$$

$$\delta\rho_2 \approx \delta\gamma\rho h'(\gamma_r), \tag{A15}$$

the selection coefficient S_{ri} describing the effect of reproductive interference is given by

$$S_{ri} = c_{RI} \frac{\tilde{N}}{N} \rho \Bigg(-h'(1-\gamma_r) \left(P_{P_1} - \frac{1}{2} \right) \left(P_{T_1} - \tilde{P}_{T_1} \right) + h'(\gamma_r) \left(P_{P_2} - \frac{1}{2} \right) \left(P_{T_2} - \tilde{P}_{T_2} \right) \Bigg). \tag{A16}$$

Opportunity costs affect mutant fate

The effect of opportunity costs on mutant frequency change is given by

$$\Delta^{\text{dir-c}} P_M = - G_M \frac{c}{2} \frac{N+\tilde{N}}{N} \Big(\delta\rho_1 \left(P_{P_1}(1-P_{T_1}) + (1-P_{P_1})P_{T_1} \right) + \delta\rho_2 \left(P_{P_2}(1-P_{T_2}) + (1-P_{P_2})P_{T_2} \right) \Big). \tag{A17}$$

The fate of a mutant depends on the match at each trait between the most preferred trait value and the most common trait value.

The selection coefficient S_c describing the effect of opportunity costs is thus given by

$$S_c = - \frac{c}{2} \frac{N+\tilde{N}}{N} \rho \Big(- h'(1-\gamma_r) \left(P_{P_1}(1-P_{T_1}) + (1-P_{P_1})P_{T_1} \right) + h'(\gamma_r) \left(P_{P_2}(1-P_{T_2}) + (1-P_{P_2})P_{T_2} \right) \Big). \tag{A18}$$

Indirect selection promotes preference on the trait providing the most substantial indirect fitness benefit

The term describing the effect of indirect selection on mutant alleles at locus M is given by

$$\Delta^{\text{ind}} P_M = \overbrace{D^*_{T_1 M}}^{\substack{\text{genetic association} \\ \text{between } T_1 \text{ and } M}} \overbrace{\left(s_1 + \overline{\rho}_1 (P_{P_1} - \frac{1}{2}) \right)}^{\text{direct selection on } T_1} + \underbrace{D^*_{T_2 M}}_{\substack{\text{genetic association} \\ \text{between } T_2 \text{ and } M}} \underbrace{\left(s_2 + \overline{\rho}_2 (P_{P_2} - \frac{1}{2}) \right)}_{\text{direct selection on } T_2}, \tag{A19}$$

where $D^*_{T_1 M}$ (resp. $D^*_{T_2 M}$) is the genetic association between the mutant allele at locus M and allele 1 at locus T_1 (resp. T_2), see (A20). When the mutant is associated with a trait value, direct selection on this trait indirectly affects the change of mutant frequency.

The genetic association between the mutant at locus M and the trait T_i, for $i \in \{1, 2\}$, is given by

$$D^*_{T_i M} = G_{T_i} G_M \delta\rho_i \left(P_{P_i} - \frac{1}{2} \right) + O(\varepsilon^2). \tag{A20}$$

When the mutant leads to more attention on T_i ($\delta\rho_i > 0$), the mutant becomes associated with the allele associated with the most preferred trait value at T_i. Accordingly, when the mutant leads to less attention on T_i ($\delta\rho_i < 0$), it is associated with the allele associated with the least preferred trait value at T_i.

The selection coefficients S_{os} and S_{or} describing the effect of offspring survival and reproductive success are thus given by

$$S_{os} = \rho \Big(- G_{T_1} h'(1-\gamma_r) \left(P_{P_1} - \frac{1}{2} \right) s_1 + G_{T_2} h'(\gamma_r) \left(P_{P_2} - \frac{1}{2} \right) s_2 \Big), \tag{A21}$$

and

$$S_{or} = \rho^2 \Bigg(- G_{T_1} h'(1-\gamma_r) \left(P_{P_1} - \frac{1}{2} \right) h(1-\gamma_r)(P_{P_1} - \frac{1}{2}) + G_{T_2} h'(\gamma_r) \left(P_{P_2} - \frac{1}{2} \right) h(\gamma_r)(P_{P_2} - \frac{1}{2}) \Bigg). \tag{A22}$$

A2 Table and Figures

Abbreviation	Description
$\mathcal{L}$	Set of different loci: $\mathcal{L} = \{T_1, P_1, T_2, P_2, M\}$.
$\mathcal{G}$	Set of different genotypes: $\mathcal{G} = \{0,1\}^5$
$f_i/\tilde{f}_i$	Frequency of genotype i in species A or B.
$P_I/\tilde{P}_I$	Frequency of allele 1 at locus I, for $I \in \mathcal{L}$, in species A or B.
$N/\tilde{N}$	Density of species A/B.
G_I	Genetic diversity at locus I in species A: $G_I = P_I(1-P_I)$ for $I \in \mathcal{L}$.
$(I)_i$	Allele at locus I of the genotype i for $(I,i) \in \mathcal{L} \times \mathcal{G}$.
$D_{\mathcal{I}}$	Genetic association between alleles at loci in $\mathcal{I}$: $D_{\mathcal{I}} = \sum_{i \in \mathcal{G}} f_i \prod_{I \in \mathcal{I}} (P_I - (I)_i)$ for $\mathcal{I} \subset \mathcal{L}$.
$f_i'/f_i''/f_i'''$	Frequency of genotype i in species a after natural selection/reproduction/mutation.
s_n	Selective advantage of allele 1 at locus T_n, $n \in \{1,2\}$.
γ	Preference direction.
γ_r/γ_m	Preference direction associated with the resident/mutant allele.
γ_{t_0}	Ancestral preference direction.
h	Trade-off function determining the relative focus of females on either trait displayed by males.
a	Trade-off parameter tuning the shape of the function h
ρ	Strength of female preference.
c_{RI}	Strength of reproductive interference.
c	Cost of choosiness.
u_I	Mutation rate at locus $I \in \mathcal{L}$.

Table A1: Description of variables and parameters used in the model.

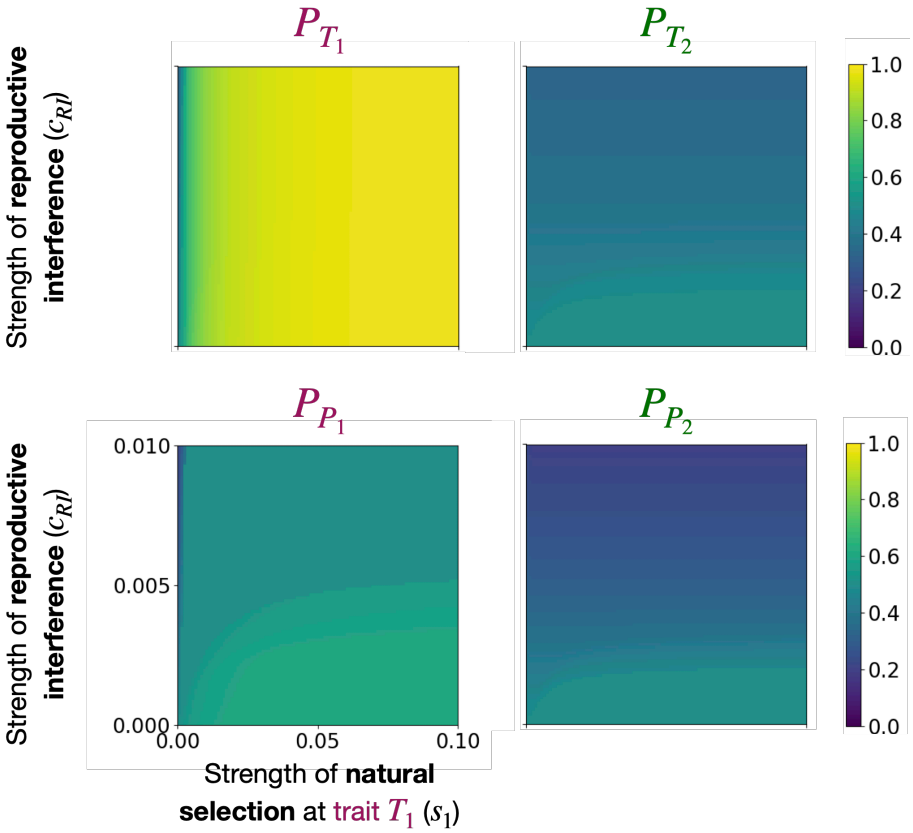

Figure A1: **Frequency of allele 1 at loci T_1, T_2, P_1 and P_2 at equilibrium preference ($\gamma_r = \gamma^*$), depending on the strength of natural selection acting on trait T_1 (s_1) and the strength of reproductive interference (c_{RI}), when T_2 is neutral ($s_2 = 0$).**

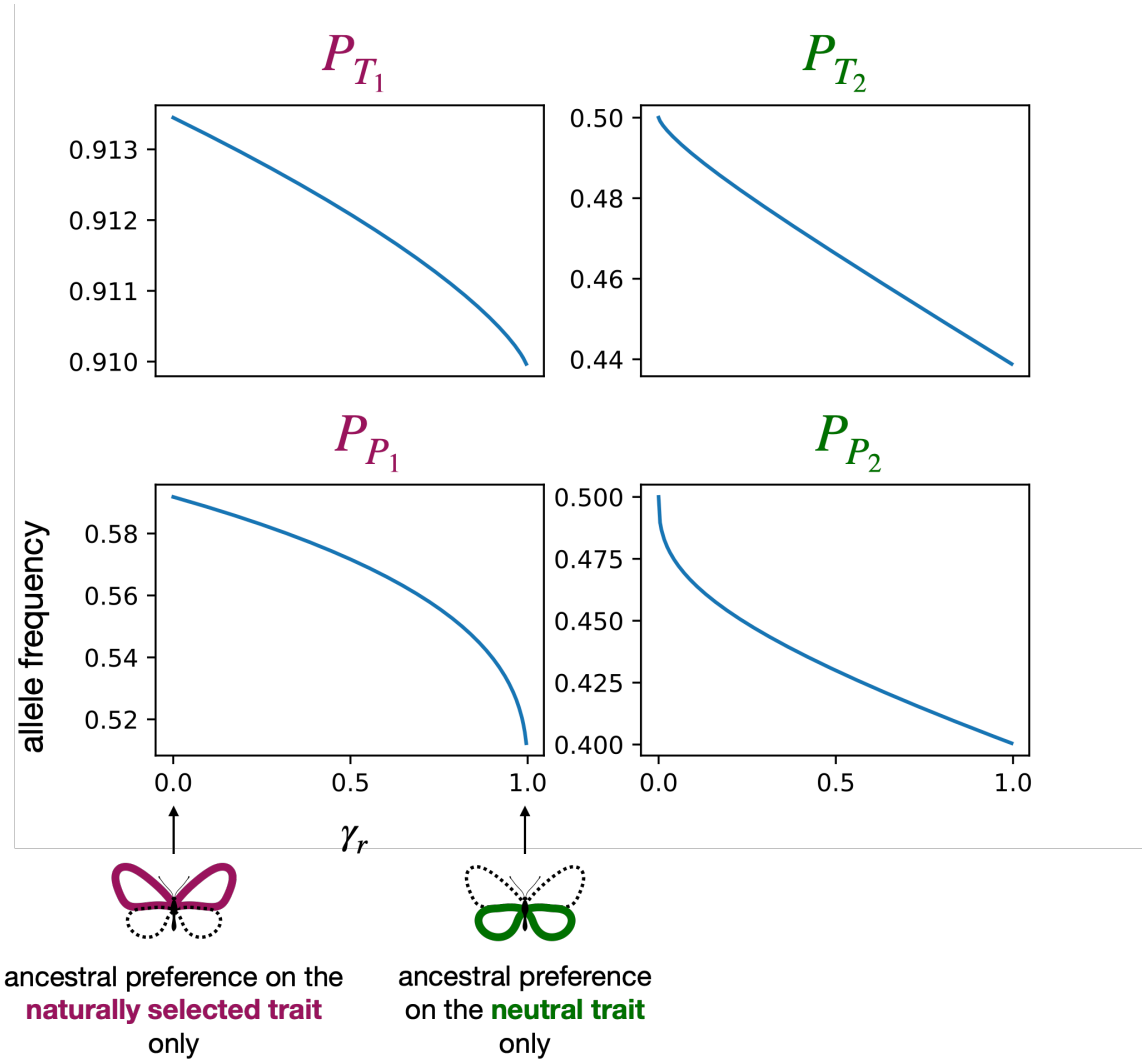

Figure A2: **Frequency of allele 1 at loci T_1, T_2, P_1 and P_2 depending on the resident preference direction.** We assume reproductive interference ($c_{RI} = 0.001$), that trait T_1 is under natural selection ($s_1 = 0.05$) and trait T_2 is neutral ($s_2 = 0$).

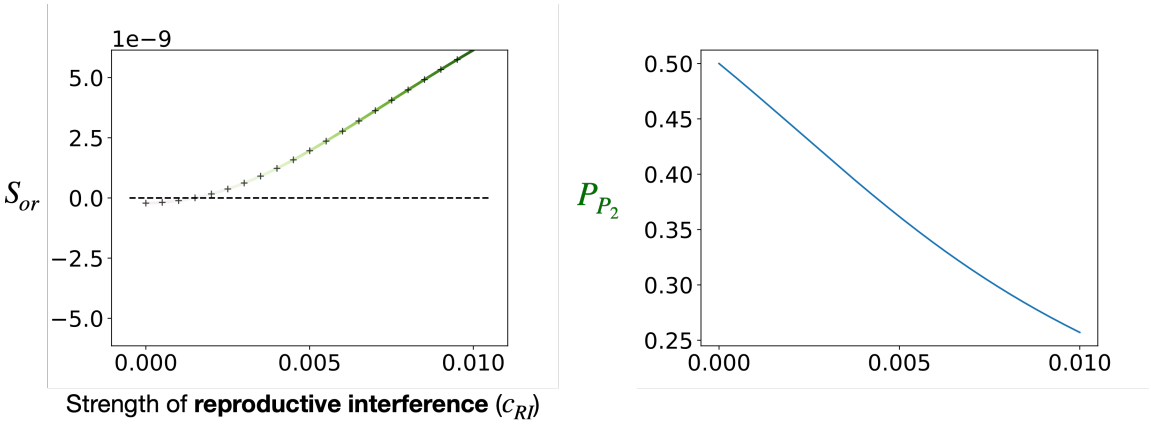

Figure A3: **Ancestral selection coefficient associated with offspring reproductive success (S_{or}) and frequency of allele 1 at locus P_2 (P_{P_2}) depending on the strength of reproductive interference (c_{RI}).** We assume ancestral preference targeting equally both traits ($\gamma_{t_0} = 0.5$). We assume reproductive interference ($c_{RI} = 0.025$), that trait T_1 is under natural selection ($s_1 = 0.02$) and trait T_2 is neutral ($s_2 = 0$). When the line is green offspring reproductive success promotes the evolution of preference towards the neutral selection T_2. The more intense the color the more intense the selection.

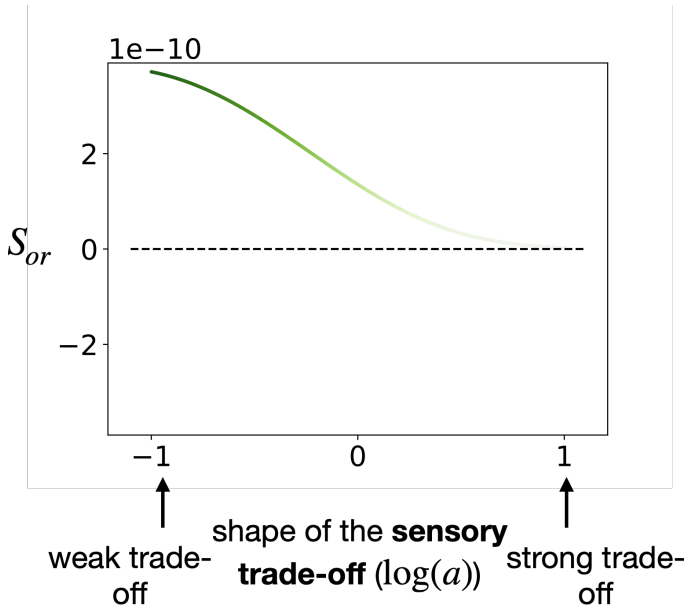

Figure A4: **Ancestral selection coefficient associated with offspring reproductive success (S_{or}) depending on the shape of the trade-off function (through the parameter a).** We assume ancestral preference targeting equally both traits ($\gamma_{t_0} = 0.5$). We assume reproductive interference ($c_{RI} = 0.025$), that trait T_1 is under natural selection ($s_1 = 0.02$) and trait T_2 is neutral ($s_2 = 0$). When the line is green offspring reproductive success promotes the evolution of preference towards the neutral selection T_2. The more intense the color the more intense the selection.

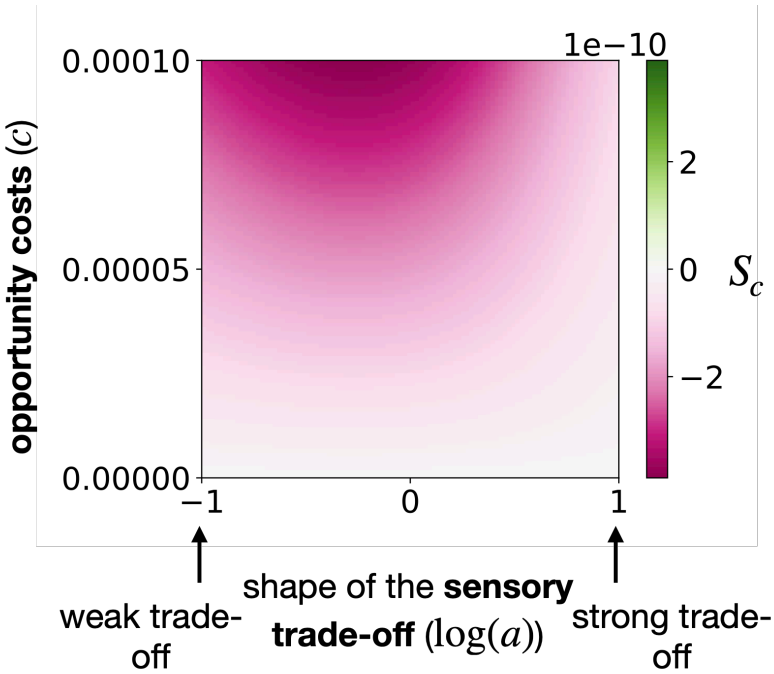

Figure A5: **Ancestral selection coefficient associated with opportunity costs (S_c).** We investigate different shapes of the trade-off function (through the parameter a) and cost of choosiness c. We assume ancestral preference targeting equally both traits ($\gamma_{t_0} = 0.5$). We assume reproductive interference ($c_{RI} = 0.025$), that trait T_1 is under natural selection ($s_1 = 0.02$) and trait T_2 is neutral ($s_2 = 0$). Purple area indicates that opportunity costs promotes the evolution of preference towards the trait under selection T_1.