Evolutionary origins of sexual dimorphism : Lessons from female-limited mimicry in butterflies.

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Abstract

2 The surprising female-limited mimicry observed in some species is a text-book example of sexually-dimorphic trait submitted to intense natural selection. Two main hypotheses have been proposed
4 to explain female-limited mimicry in butterflies. Predation pressure favouring mimicry could be higher in females because of their slower flight, and overcome developmental constraints favouring
6 the ancestral trait that limits the evolution of mimicry in males but not in females. Alternatively, the evolution of mimicry in males could be limited by sexual selection, generated by females preference
8 for non-mimetic males. However, the evolutionary origin of female preference for non-mimetic males remains unclear. Here, we hypothesise that costly sexual interactions between individuals from
10 distinct sympatric species might intensify because of mimicry, therefore promoting female preference for non-mimetic trait. Using a mathematical model, we compare the evolution of female-limited
12 mimicry when assuming either alternative hypotheses. We show that the patterns of divergence of male and female trait from the ancestral traits can differ between these selection regimes but
14 we specifically highlight that divergence in females trait is not a signature of the effect of natural selection. Altogether, our model reveals the complex interplay between sexual and natural selection
16 shaping the evolution of sexually-dimorphic traits.

Introduction

18 The evolutionary forces involved in the emergence of sexual dimorphism in different animal species are still debated. As highlighted by Wallace [1865], divergent natural selection could drive the evo-
20 lution of strikingly different phenotypes in males and females, because they may occupy different ecological niches. Sexual selection exerted by females is also a powerful force leading to the emer-
22 gence of elaborated traits in males only, therefore leading to sexual dimorphism [Darwin, 1871]. The relative contributions of natural and sexual selections to the evolution of sexually dimorphic
24 traits has generated important controversies. The evolution of sexual dimorphism in wing colour patterns in butterflies has been central to this debate because wing colour patterns are under strong
26 natural selection by predators and are also involved in mate choice and species recognition [Turner, 1978]. Quantifying phenotypic divergence in males and females from the ancestral trait may allow
28 to identify the main evolutionary factors involved in the evolution of sexual dimorphism. Using a phylogenetic approach on European butterflies, van der Bijl et al. [2020] recently showed that the
30 wing colour pattern dimorphism is mainly driven by the divergence of male phenotype, in line with

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the sexual selection hypothesis. In contrast to this general trend, sexual dimorphism where females exhibit a derived colour pattern is frequently observed in butterfly species involved in Batesian mimicry [Kunte, 2008]. In these palatable species, the evolution of colour patterns looking similar to the phenotype displayed in chemically-defended species living in sympatry is strongly promoted: because predators associate conspicuous colouration to defences, individuals displaying mimetic colouration in palatable species have a limited predation risk [Bates, 1981, Ruxton et al., 2019]. Despite predation affecting individuals from both sexes, mimicry is sometimes surprisingly limited to females [Ford, 1975, Kunte, 2008, Nishikawa et al., 2015], therefore begging the question of the evolutionary forces preventing the evolution of mimicry in males.

Because butterfly males and females generally differ in their behaviour, the strength of predation pressure might differ among sexes [Ohsaki, 1995, 2005]: for instance, females usually spend a lot of time ovipositing on specific host-plants, and thus have a more predictable behaviour for predators. Moreover, flight speed is generally higher in males than females: females are heavier because they carry eggs [Gilchrist, 1990], and males have higher relative thorax mass [Karlsson and Wickman, 1990] and muscle mass [Marden and Chai, 1991], resulting in increased flight power [Chai and Srygley, 1990]. Predation pressures are thus expected to be stronger in females. Wing pattern evolution is also shaped by developmental constraints [Van Belleghem et al., 2020] that may impede divergence from the ancestral trait. Such trade-off between developmental constraints favouring the ancestral trait and selection promoting mimicry might differ between sexes: if predation is lower in males, the constraints limiting mimicry may overcome the benefit from mimicry in males, whereas in females the higher predation pressure may promote mimicry. Nevertheless, evidence for the limited predation in males as compared to females is controversial [Wourms and Wasserman, 1985] suggesting that contrasted predation in males and females could not be the main driver of female-limited mimicry (named FLM hereafter).

Other constraints triggered by sexual selection might limit mimicry in males. In the female-limited Batesian mimic *Papilio polyxenes asterius*, experimental alteration of male colour pattern into female colour pattern leads to lower success during male-male encounters and increased difficulty in establishing a territory, therefore reducing mating opportunities [Lederhouse and Scriber, 1996]. Furthermore, in the female-limited Batesian mimic *Papilio glaucus*, females prefer control painted non-mimetic males over painted mimetic males [Krebs and West, 1988]. Wing colour patterns in mimetic butterflies may therefore modulate male reproductive success, by influencing both male-male competition and mating success with females. In particular, females preference for ancestral trait may generate sexual selection limiting male mimicry [Belt, 1874., Turner, 1978]. Nevertheless, because mimetic colouration is under strong positive selection, females preference are predicted to favour mimetic colouration in males, as observed in species involved in Müllerian mimicry, *i.e.* when co-mimetic species are all chemically-defended [Jiggins et al., 2001, Naisbit et al., 2001, Kronforst et al., 2006, Merrill et al., 2014]. It is thus unclear what does limit the evolution of females preference towards mimetic colouration in males from species involved in Batesian mimicry.

Females preference for mimetic males may be disadvantageous because this behaviour may lead to mating interactions with unpalatable 'model' species. Therefore reproductive interference (named RI hereafter), *i.e.* costly interactions between different species during mate acquisition (see [Gröning and Hochkirch, 2008] for a definition), may impair the evolution of females preference towards mimetic colour patterns displayed by other sympatric species. The evolution of mimetic colouration in males may indeed increase costs linked to RI in females, and therefore promote the evolution of preference for non-mimetic traits in males. Such RI has been observed between species sharing similar aposematic traits (in *Heliconius* and *Mechanitis* species [Estrada and Jiggins, 2008]).

The rate of erroneous mating may be limited by the difference in male pheromones between mimetic species (see Darragh et al. [2017], González-Rojas et al. [2020] for empirical examples in *Heliconius* butterflies). However, females may still suffer from cost associated to RI, even if they refuse mating with heterospecific males: females may allow courting by heterospecific males displaying their preferred cue, resulting in increased investment in mate searching (see signal jamming in [Gröning and Hochkirch, 2008]). Pheromones may not limit this increase of investment in mate searching, because they act as short-distance cue that may be perceived only during the courtship [Mérot et al., 2015]. Females deceived by the colour pattern then need to deploy substantial efforts to avoid the heterospecific mating. Theoretical studies highlight that RI promotes the evolution of females preference different from the phenotype of the other sympatric species because it reduces the number of costly sexual interactions [McPeek and Gavrilets, 2006, Yamaguchi and Iwasa, 2013, Maisonneuve et al., 2021]. These females preference, caused by RI may therefore explain the evolution of sexual dimorphism in mimetic species [Yamaguchi and Iwasa, 2013].

Interestingly, the two main hypotheses usually explaining FLM, *i.e.* (1) sexually contrasted predation and (2) sexual selection on males, are both equally relevant for palatable as well as unpalatable species. Indeed, sympatric unpalatable species frequently display a common mimetic trait [Sherratt, 2008], suggesting a strong selection promoting mimicry. However, FLM is considered to be widespread in palatable species but rare in unpalatable ones [Mallet and Joron, 1999] (but see [Nishida, 2017]). This suggests that the evolution of sexual dimorphism in mimetic species might depend on the level of defences.

Here, we investigate how (1) RI and (2) sexually contrasted predation may promote the evolution of FLM using a mathematical model. Firstly we pinpoint the specific evolutionary outcomes associated with the emergence of FLM driven by RI or sexually contrasted predation, therefore providing relevant predictions for comparisons with empirical data. Secondly, we study the impact of unpalatability levels on the emergence of sexual dimorphism, to test whether FLM may be restricted to palatable species. Our model describes the evolution of quantitative traits, following the framework established by Lande and Arnold [1985] in a *focal* species, living in sympatry with a defended *model* species. We specifically study the evolution of (1) the quantitative traits displayed in males t_m and females t_f involved in mimetic interactions, (2) the preference of females for the different values of males trait p_f. We assume that individuals in the *focal* species gain protection against predators from the similarity of their warning trait towards the trait displayed by the unpalatable *model* species. However, trait similarity between species generates fitness costs of RI paid by females from the *focal* species [McPeek and Gavrilets, 2006, Yamaguchi and Iwasa, 2013]. We assume that matings between individuals from the *focal* and the *model* species never produce any viable hybrid. We also consider constraints limiting mimicry promoting the ancestral trait value in the *focal* species, by assuming selection promoting the ancestral trait value t_a. Using a weak selection approximation [Barton and Turelli, 1991, Kirkpatrick et al., 2002], we obtain equations describing the evolution of the mean trait and preference values. We then use numerical analyses to investigate (1) the role of RI in FLM and (2) the effect of the level of unpalatability in the *focal* species on the emergence of FLM.

Model

We consider a single *focal* species living in sympatry with a defended species (referred to as the *model* species hereafter). Within the *model* species, all individuals display the same warning signal. We investigate the evolution of the warning trait expressed in the *focal* species, influenced by

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both (1) predators behaviour promoting mimicry towards the *model* species and (2) mate choice exerted by females on the trait expressed by males. We assume that female is the choosy sex, implying an asymmetry in the selection pressure exerted on male and female traits, potentially favouring the emergence of a sexual dimorphism. We thus study the traits t_m and t_f expressed in males and females respectively, as well as the mate preference expressed by females towards males displaying trait value p_f. In contrast, both males and females of the *model* species display traits closed to the mean value $\bar{t}'$, assumed to be fixed. Individuals of the *focal* species then benefit from increased survival when they display a trait similar to the trait expressed in the *model* species $(\bar{t}')$, because of the learning behaviour of predators. This resemblance towards the *model* species then induces costs for individuals from the *focal* species, caused by reproductive interference (RI). These RI costs depend on the discrimination capacities and mate preferences of females and on the phenotypic distances between (1) the traits displayed by males from the *focal* species and (2) the traits expressed in males from the *model* species.

We assume that the traits and preference in the *focal* species are quantitative traits, with an autosomal, polygenic basis with additive effects [Iwasa et al., 1991]. We assume that the distribution of additive effects at each locus is a multivariate Gaussian [Lande and Arnold, 1985]. We consider discrete and non-overlapping generations. Within each generation, natural selection acting on survival and sexual selection acting on reproductive success occur successively. Natural selection acting on an individual depends on the trait t expressed. We note $W_{ns}^{\male}(t_m)$ and $W_{ns}^{\female}(t_f)$ (defined after in equations (6) and (7)) the fitness components due to natural selection acting on a male of trait t_m and a female of trait t_f respectively. To compute the fitness component due to reproduction, we then note $W_r(t_m, p_f)$ (defined after in equation (21)) the contribution of a mating between a male with trait t_m and a female with preference p_f to the next generation. This quantity depends on (1) female mating preference, (2) male trait and (3) RI with the *model* species. The fitness of a mated pair of a male with trait t_m and a female with trait t_f and preference p_f is given by:

$$W(t_m, t_f, p_f) = W_{ns}^{\male}(t_m) W_r(t_m, p_f) W_{ns}^{\female}(t_f). \tag{1}$$

Using the Price's theorem [Rice, 2004], we can approximate the change in the mean values of traits $\bar{t}_m, \bar{t}_f$ and preference $\bar{p}_f$ in the *focal* species after the natural and sexual selection respectively by:

$$\begin{pmatrix} \Delta\bar{t}_m \\ \Delta\bar{t}_f \\ \Delta\bar{p}_f \end{pmatrix} = \frac{1}{2} \begin{pmatrix} G_{t_m t_m} & G_{t_m t_f} & G_{t_m p_f} \\ G_{t_m t_f} & G_{t_f t_f} & G_{t_f p_f} \\ G_{t_m p_f} & G_{t_f p_f} & G_{p_f p_f} \end{pmatrix} \begin{pmatrix} \beta_{t_m} \\ \beta_{t_f} \\ \beta_{p_f} \end{pmatrix}, \tag{2}$$

where for $i \in \{t_m, t_f, p_f\}$, G_{ii} is the genetic variance of i and for $i, j \in \{t_m, t_f, p_f\}$ with $i \neq j$ G_{ij}, is the genetic covariance between i and j and with

$$\begin{pmatrix} \beta_{t_m} \\ \beta_{t_f} \\ \beta_{p_f} \end{pmatrix} = \begin{pmatrix} \frac{d}{dt_m} \log\left(W(t_m, t_f, p_f)\right) \\ \frac{d}{dt_f} \log\left(W(t_m, t_f, p_f)\right) \\ \frac{d}{dp_f} \log\left(W(t_m, t_f, p_f)\right) \end{pmatrix} \Bigg|_{(t_m, t_f, p_f) = (\bar{t}_m, \bar{t}_f, \bar{p}_f)}, \tag{3}$$

being the selection vector describing the effect of natural and sexual selections on mean traits and preference (see Appendix 1).

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We assume weak natural and sexual selections [Iwasa et al., 1991, Pomiankowski and Iwasa, 1993], *i.e.* that the difference of fitness between different individuals is at maximum of order ε, with ε being small. Under this hypothesis genetic correlations generated by selection and non random mating quickly reach equilibrium [Nagylaki, 1993] and can thus be approximated by their equilibrium values. Weak selection hypothesis also implies that the variance of traits and preference is low [Iwasa et al., 1991].

Following [Iwasa et al., 1991], we assume that for $i \in \{t_m, t_f, p_f\}$, G_{ii} is a positive constant maintained by an equilibrium between selection and recurrent mutations. We assume $G_{t_m t_f}$ to be constant: because neither selection nor nonrandom mating generate association between t_m and t_f this quantity depends only on the genetic architecture coding for traits expressed in males and females. For example $G_{t_m t_f} = 0$ would describe a situation where t_m and t_f are controlled by different sets of loci. Non-null value of $G_{t_m t_f}$ would mean that t_m and t_f have (at least partially) a common genetic basis.

We assume that traits t_m and t_f have different genetic bases than preference p_f. Thus only non-random mating generates genetic association between t_m and p_f. Under weak selection hypothesis $G_{t_m p_f}$ is assumed to be at equilibrium. This quantity is given by (see Appendix 2):

$$G_{t_m p_f} = a G_{t_m t_m} G_{p_f p_f}, \tag{4}$$

where a quantifies how much do females reject males displaying non-preferred trait (see hereafter).

Because neither selection nor nonrandom mating generate association between t_f and p_f, following equation (4a) in Lande and Arnold [1985], we have

$$G_{t_f p_f} = \frac{G_{t_m t_f} G_{t_m p_f}}{G_{t_m t_m}}. \tag{5}$$

Ancestral trait value t_a

To investigate the effect of RI on the evolution of sexual dimorphism, we study the evolution of male and female traits (t_m and t_f) in the *focal* species, from an ancestral trait value initially shared between sexes (t_a). This ancestral trait value t_a represents the optimal trait value in the *focal* species, without interaction with the *model* species. This optimal value is assumed to be shaped by developmental as well as selective constraints, specific to the *focal* species. The natural selection exerted on males and females then depends on (1) departure from the ancestral trait value t_a, inducing a selective cost s, as well as (2) protection against predators brought by mimicry, captured by the term $W_{pred}^{\male}$ and $W_{pred}^{\female}$ for males and females respectively. It is thus given by:

$$W_{ns}^{\male}(t_m) = W_{pred}^{\male}(t_m) \exp\left[-s(t_m - t_a)^2\right], \tag{6}$$

$$W_{ns}^{\female}(t_f) = W_{pred}^{\female}(t_f) \exp\left[-s(t_f - t_a)^2\right]. \tag{7}$$

Predation pressure exerted on warning trait

Predators exert a selection on individual trait promoting resemblance to the *model* species, resulting in an effect on fitness W_{pred}. Müllerian mimicry indeed generates positive density-dependent selection [Benson, 1972, Mallet and Barton, 1989, Chouteau et al., 2016], due to predators learning. The density-dependence is modulated by the individual defence level λ, shaping predator deterrence:

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the higher the defence, the higher the defended individual contributes to the learning of predators. We note λ' the defence level of an individual in the *model* species. We assume that harmless individuals ($\lambda = 0$) neither contribute to predators learning, nor impair it. The protection gained against predators then depends on the level of resemblance (as perceived by predators) among defended prey only, and on the number of defended individuals sharing the same signal. We note N and N' the densities of individuals in the *focal* species and in the *model* species, respectively, and we assume a balanced sex ratio. The level of protection gained by an individual with trait t because of resemblance with other individuals is given by:

$$
\mathcal{D}(t) = \overbrace{\int_{\tau_m} \lambda \frac{N}{2} f^{\male}(\tau_m) \exp\left[-b(t-\tau_m)^2\right] \mathrm{d}\tau_m}^{\substack{\text{protection gained by resemblance} \\ \text{with males of the \textit{focal} species}}} + \overbrace{\int_{\tau_f} \lambda \frac{N}{2} f^{\female}(\tau_f) \exp\left[-b(t-\tau_f)^2\right] \mathrm{d}\tau_f}^{\substack{\text{protection gained by resemblance} \\ \text{with females of the \textit{focal} species}}}
$$
$$
+ \underbrace{\int_{t'} \lambda' N' g(t') \exp\left[-b(t-t')^2\right] \mathrm{d}t'}_{\substack{\text{protection gained by resemblance} \\ \text{with individuals of the \textit{model} species}}},
\tag{8}
$$

where $\exp\left[-b(t-\tau)^2\right]$ describes how much predators perceive the trait values t and τ as similar. The predators discrimination coefficient b thus quantifies how much predators discriminate different trait values displayed by prey. $f^{\male}$, $f^{\female}$ and g are the distribution of traits in males and females of the *focal* species and in the *model* species respectively.

Assuming that the distribution of traits has a low variance within both the *focal* and the *model* species leads to the following approximation (see Appendix 3):

$$
\mathcal{D}(t) \approx \lambda \frac{N}{2} \exp\left[-b(t-\bar{t}_m)^2\right] + \lambda \frac{N}{2} \exp\left[-b(t-\bar{t}_f)^2\right] + \lambda' N' \exp\left[-b(t-\bar{t}')^2\right].
\tag{9}
$$

Because males and females can display different traits, the protection brought by mimicry might differ between sexes. Moreover, because males and females may have different behaviours and morphologies the strength of predation pressure can also vary between sexes. We note $d_m, d_f \in (0,1)$ the basal predation rates for males and females respectively and we assume these parameters to be of order ε, with ε small, in line with the weak selection hypothesis. The impacts of predation on the fitness of a male and a female displaying the trait value t_m and t_f are given by:

$$
W^{\male}_{pred}(t_m) = \exp\left\{\frac{-d_m}{1+\mathcal{D}(t_m)}\right\} \quad \text{and} \quad W^{\female}_{pred}(t_f) = \exp\left\{\frac{-d_f}{1+\mathcal{D}(t_f)}\right\}.
\tag{10}
$$

Mating success modulating the evolution of female preference and male trait

The evolution of trait and preference also depends on the contribution to the next generation of crosses between males with trait t_m and females with preference p_f, $W_r(t_m, p_f)$. Because predators behaviour favours mimicry between sympatric species, substantial RI may occur in the *focal* species, because of erroneous species recognition during mate searching. Such RI depends on (1) females preference towards the warning trait displayed by males, (2) the distribution of this warning trait in males from both the *focal* and the *model* species and (3) the capacity of females to recognise

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conspecific males using alternative cues (pheromones for example). In the model, the investment of females in interspecific mating interaction is captured by the parameter $c_{RI} \in [0, 1]$. This cost of RI incurred to the females can be reduced when female choice is also based on alternative cues differing between mimetic species. When a female with preference p_f encounters a male displaying the trait value t_m, the mating occurs with probability

$$\exp\left[-a(p_f - t_m)^2\right], \tag{11}$$

when the encountered male is a conspecific or

$$c_{RI} \exp\left[-a(p_f - t_m)^2\right], \tag{12}$$

when the encountered male belongs to the *model* species. Females choosiness a, assumed constant among females, quantifies how much do females reject males displaying a non-preferred trait.

During an encounter, the probability that a female with preference p_f accepts a conspecific male is then given by [Otto et al., 2008]:

$$T(p_f) = \int_{t_m} \overbrace{\frac{N}{N + N'} f^{\male}(t_m)}^{\substack{\text{probability of encountering} \\ \text{a conspecific male} \\ \text{with trait } t_m}} \overbrace{\exp\left[-a(p_f - t_m)^2\right]}^{\substack{\text{probability of accepting} \\ \text{a conspecific male} \\ \text{with trait } t_m}} \, dt_m. \tag{13}$$

A female with preference p_f may also accept an heterospecific male with probability:

$$T_{RI}(p_f) = \int_{t'} \overbrace{\frac{N'}{N + N'} g(t')}^{\substack{\text{probability of encountering} \\ \text{an heterospecific male} \\ \text{with trait } t'}} \overbrace{c_{RI} \exp\left[-a(p_f - t')^2\right]}^{\substack{\text{probability of accepting} \\ \text{an heterospecific male} \\ \text{with trait } t'}} \, dt'. \tag{14}$$

Assuming that the distribution of traits has a low variance within both the *focal* and the *model* species leads as before to the following approximations:

$$T(p_f) \approx \frac{N}{N + N'} \exp\left[-a(p_f - \bar{t}_m)^2\right], \tag{15}$$

and

$$T_{RI}(p_f) \approx \frac{N'}{N + N'} c_{RI} \exp\left[-a(p_f - \bar{t}')^2\right]. \tag{16}$$

We assume that heterospecific crosses never produce any viable offspring, and that females engaged in such matings cannot recover this fitness loss (see Figure 1). Only crosses between conspecifics produce viable offspring (see Figure 1). Knowing that a female with preference p_f has mated with a conspecific male, the probability that this male displays the trait t_m is given by:

$$\phi(p_f, t_m) = \frac{\exp\left[-a(p_f - t_m)^2\right] f^{\male}(t_m)}{\int_{\tau_m} \exp\left[-a(p_f - \tau_m)^2\right] f^{\male}(\tau_m) \, d\tau_m}. \tag{17}$$

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Using again the assumption that the trait distribution has a low variance, this can be approximated by

$$\phi(p_f, t_m) \approx \frac{\exp\left[-a(p_f - t_m)^2\right] f^{\circlearrowleft}(t_m)}{\exp\left[-a(p_f - \bar{t}_m)^2\right]}. \tag{18}$$

Considering that females only encounter one male, the proportion of crosses between a female with preference p_f and a conspecific male with trait t_m would be

$$\mathcal{P}^1(p_f, t_m) = h(p_f) T(p_f) \frac{\exp\left[-a(p_f - t_m)^2\right] f^{\circlearrowleft}(t_m)}{\exp\left[-a(p_f - \bar{t}_m)^2\right]}, \tag{19}$$

where h is the distribution of preferences in the population.

However, we assume that females refusing a mating opportunity can encounter another male with probability $1 - c$ (see Figure 1). We interpret $c \in [0, 1]$ as the cost of choosiness (similar to the coefficient c_r in [Otto et al., 2008]). The proportion of matings between a female with preference p_f and a conspecific male with trait t_m is thus given by

$$\mathcal{P}(p_f, t_m) = \sum_{i=0}^{+\infty} \left((1 - T(p_f) - T_{RI}(p_f))(1 - c)\right)^i \mathcal{P}^1(p_f, t_m)$$

$$= \frac{\mathcal{P}^1(p_f, t_m)}{c + (1 - c)(T(p_f) + T_{RI}(p_f))}, \tag{20}$$

where $\left((1 - T(p_f) - T_{RI}(p_f))(1 - c)\right)^i$ is the probability that a female with preference p_f rejects the i males she first encounters and then encounters an $(i + 1) - th$ male.

The contribution to the next generation of a mating between a male with trait t_m and a female with trait p_f, $W_r(t_m, p_f)$ is thus given by (see Figure 1)

$$W_r(t_m, p_f) = \frac{T(p_f)}{c + (1 - c)(T(p_f) + T_{RI}(p_f))} \times \frac{\exp\left[-a(p_f - t_m)^2\right]}{\exp\left[-a(p_f - \bar{t}_m)^2\right]} \tag{21}$$

All variables and parameters used in the model are summed up in Table 1.

Relaxing the weak preference hypothesis

Because the stringency of females choice (a) is a key driver of the effect of RI on the convergence towards the trait displayed in the *model* species, we do not assume that a is always of order ε. Assuming such a strong sexual selection violates the weak selection hypothesis. However, because strong females choosiness leads to higher sexual selection, the discrepancy between females preference and males trait values ($|\bar{t}_m^* - \bar{p}_f^*|$) becomes limited. Therefore sexual selection and opportunity cost are actually weak and we can still estimate the matrix of genetic covariance and assume that the genetic variances of traits and preference are low.

Model exploration.

We assume that the *focal* species is ancestrally not in contact with the *model* species, and therefore the initial mean trait values displayed by males and females are equal to the optimal trait t_a. We
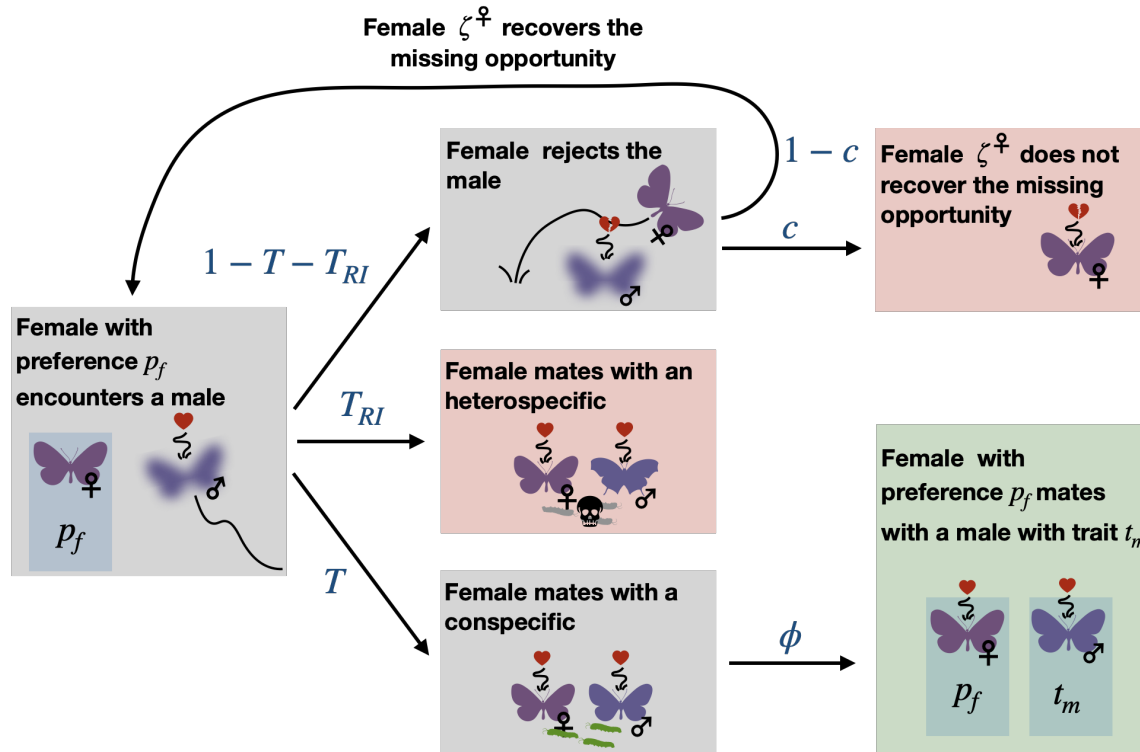
8

Figure 1: **Computation of the contribution to the next generation of a mating.** During an encounter, a female expresses her preference towards the warning trait displayed by the male and other cues that may differ between conspecific and heterospecific males. A female accepts a conspecific (resp. heterospecific) male with probability $T(p_f)$ (resp. $T_{RI}(p_f)$) (see Equation (13) (resp. (14))). A mating with an heterospecific male produces no viable offspring and the female cannot mate anymore. When the female mates with a conspecific of trait t_m, the cross occurs with probability $\phi(p_f, t_m)$. During an encounter the female may refuse a mating opportunity with a male displaying a trait value t_m distant from her preference p_f and can subsequently encounter other males with probability $1 - c$. Alternatively, she may not recover the fitness loss with probability c, resulting in an opportunity cost. The contribution to the next generation of a mating between a male with trait t_m and a female with preference p_f is thus given by $W_r(t_m, p_f)$ (see Equation (21)). Expressions in blue represent the probabilities associated with each arrow. In red, the female does not produce any offspring. In green, the mating between a male with trait t_m and a female with preference p_f happens and produces progeny.

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Abbreviation	Description
$\bar{t}_m/\bar{t}_f$	Mean trait value displayed in the *focal* species by males and females respectively
$\bar{p}_f$	Mean female preference value in the *focal* species
G	matrix of genetic covariance
a	Females choosiness in the *focal* species
s	Strength of developmental constraints in the *focal* species
t_a	Ancestral trait favoured by developmental constraints in the *focal* species
d_m/d_f	Basal predation rate in males and females respectively
b	Predators discrimination
λ/λ'	Defence level of individuals of the *focal* and *model* species respectively
N/N'	Density of the *focal* and *model* species respectively
c_{RI}	Strength of reproductive interference
c	Cost of choosiness

Table 1: Description of variables and parameters used in the model.

also assume that the mean female preference value is initially equal to the mean trait value displayed
by males. At the initial time, we assume that the *focal* species enters in contact with the *model*
species. The dynamics of traits and preference values then follow Equation (2).

Numerical simulations

We use numerical simulations to estimate the traits and preference values at equilibrium ($\bar{t}_m^*$, $\bar{t}_f^*$,
$\bar{p}_f^*$). Numerically, we consider that the traits and preference are at equilibrium when

$$\left\| \begin{pmatrix} \Delta \bar{t}_m \\ \Delta \bar{t}_f \\ \Delta \bar{p}_f \end{pmatrix} \right\|_2 < 3 \times 10^{-11}. \tag{22}$$

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

Comparing alternative mechanisms inducing female-limited mimicry

First, we compare the evolutionary outcomes when assuming two alternative mechanisms generating
FLM in an harmless species ($\lambda = 0$): (1) sexual selection generated by RI (c_{RI} and $a > 0$) and (2)
sexually contrasted predation ($d_f > d_m$). We thus compute the equilibrium traits and preference
($\bar{t}_m^*$, $\bar{t}_f^*$, $\bar{p}_f^*$) for different strengths of RI ($c_{RI} \in [0, 0.1]$) or different basal predation rate sexual
ratios between males and females $d_m/d_f \in [0, 1]$. Note that the two mechanisms are not mutually
exclusive in natural populations. However here we investigate them separately to identify the
specific evolutionary trajectories they generate. We then determine the range of key parameters
enabling the evolution of FLM, under each mechanism assumed. We specifically follow the evolution
of sexual dimorphism generated by each mechanism by comparing the level of sexual dimorphism
at equilibrium defined by $|\bar{t}_m^* - \bar{t}_f^*|$.

Differential divergence from ancestral traits in male and female causing sexual dimorphism

To investigate whether the evolution of sexual dimorphism stems from increased divergence of traits from the ancestral states of one of the two sexes, we then compute the sexual bias in phenotypic divergence defined by

$$\phi = |\bar{t}_m^* - t_a| - |\bar{t}_f^* - t_a|.$$

When $\phi < 0$ we have $|\bar{t}_f^* - t_a| > |\bar{t}_m^* - t_a|$ thus the trait diverged more in females than in males (see an illustration in Figure 2(a) and Figure 2(b)). By contrast $\phi > 0$ indicates that the trait diverged more in males than in females (see an illustration in Figure 2(c)). We compare this sexual bias in phenotypic divergence under the two hypothetical mechanisms of FLM, to determine whether this criterium could be used to infer the actual evolutionary pressures involved in the emergence of FLM in natural populations.
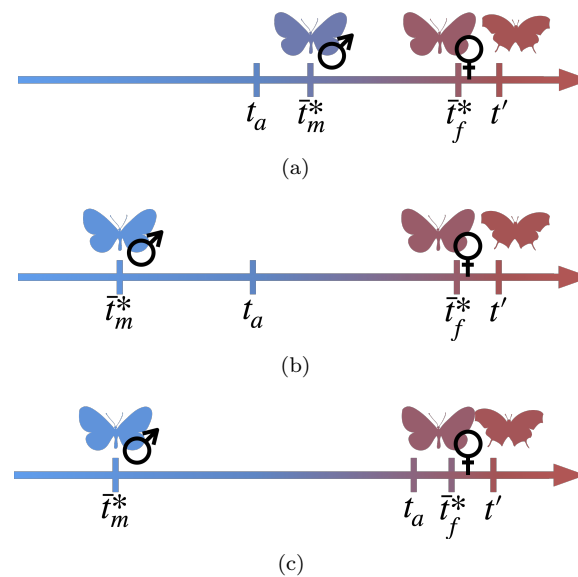
Figure 2: **Illustration of the three main outcomes:** (a) males trait value in the *focal* species gets closer to the value displayed in the *model* species t', (b) males trait value in the *focal* species diverges away from the value displayed in the *model* species t', (c) when the ancestral and the mimetic trait are close and males trait value in the *focal* species diverges away from the value displayed in the *model* species t' then the phenotypic distance with the ancestral trait is higher in males than in females.

We first study the values of sexual bias in phenotypic divergence when RI causes FLM ($c_{RI} = 0.01$), using numerical simulations. We investigate the effect of two key parameters: female choosiness a modulating cost of RI and the phenotypic distance between the ancestral trait t_a and the mimetic trait t'. To investigate the impact of the phenotypic distance between the ancestral and the mimetic traits, we fixed the mimetic trait value to 1 ($t' = 1$) and vary the ancestral trait value ($t_a \in [0, 1]$) (see illustration in Figures 2(b) and 2(c)). We then study the sexual bias in phenotypic

326 divergence when FLM stems from sexually contrasted predation ($d_f > d_m$), by deriving analytical results standing for all parameters value (see Appendix 6).

328 **Investigating the impact of the defence level on the evolution of female-limited mimicry**

Because FLM is usually reported for Batesian mimics, we then investigate the impact of the defence

330 level ($\lambda \in [0, 0.1]$) on equilibrium traits ($\bar{t}_m^*$, $\bar{t}_f^*$) and the level of sexual dimorphism ($\bar{t}_m^* - \bar{t}_f^*$). Because males and females in the *focal* species can display different traits, the level of protection

332 gained by individuals of one sex through mimicry depends on males and females resemblance to the *model* species but also on the density of individuals of that sex within the *focal* species, modulated

334 by the individual level of defence in the *focal* species (λ). When males from the *focal* species are non-mimetic, their defence level is given by the individual level of defence λ and the density of males

336 $N/2$. To investigate the impact of defence level on the emergence of FLM, we thus explore not only the effect of the individual defence level λ but also of the density of the *focal* species ($N \in [0, 20]$).

338 The effects of all explored parameters and evolutionary forces on the evolution of FLM are summed up in Figure 3.
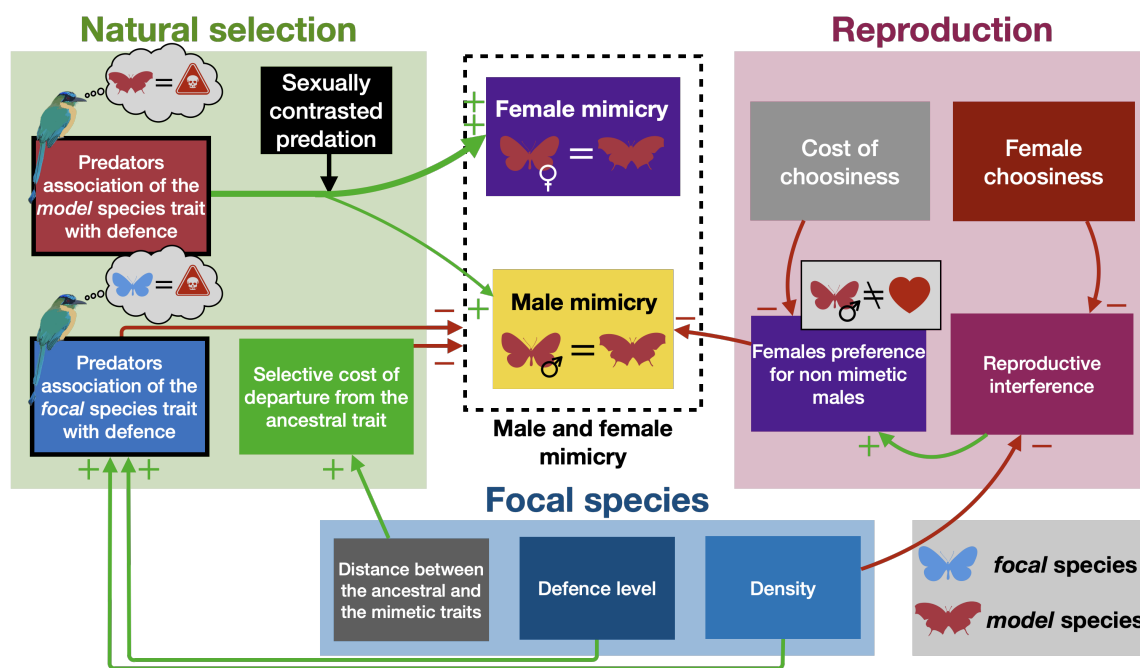
Figure 3: Summary of the impact of selective forces and parameters on the evolution of female-limited mimicry. Green and red arrows represent the positive and negative impact respectively.

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Results

RI promotes female-limited mimicry in palatable species

We first test whether RI can generate FLM in a harmless species ($\lambda = 0$). We thus investigate the impact of the strength of RI (c_{RI}) on the evolution of males trait ($\bar{t}_m^*$), females trait and preference ($\bar{t}_f^*$ and $\bar{p}_f^*$), for different levels of females choosiness (a) modulating the costs generated by the strength of RI (Figure 4(a)). Without RI ($c_{RI} = 0$), both males and females in the *focal* species are mimetic at equilibrium and the sexual dimorphism therefore does not emerge (Figure 4(a)). By contrast, when assuming RI ($c_{RI} > 0$), FLM evolves in the *focal* species (Figure 4(a)). RI promotes a greater distance between final females preference $\bar{p}_f^*$ and the trait of the *model* species t'. Such females preference for non-mimetic males reduces costly sexual interactions with heterospecific males of the *model* species and generates sexual selection on males trait, inhibiting mimicry in males. Because FLM strongly depends on the evolution of females preference for potentially scarce non-mimetic males, it emerges only when the cost of choosiness (c) is low (see Appendix 4 for more details). FLM evolves only when male and female traits have at least partially different genetic basis, allowing divergent evolution between sexes. The genetic covariance between males and females trait $G_{t_m t_f}$ then only impacts the time to reach the equilibrium (see Appendix 5 for more details).
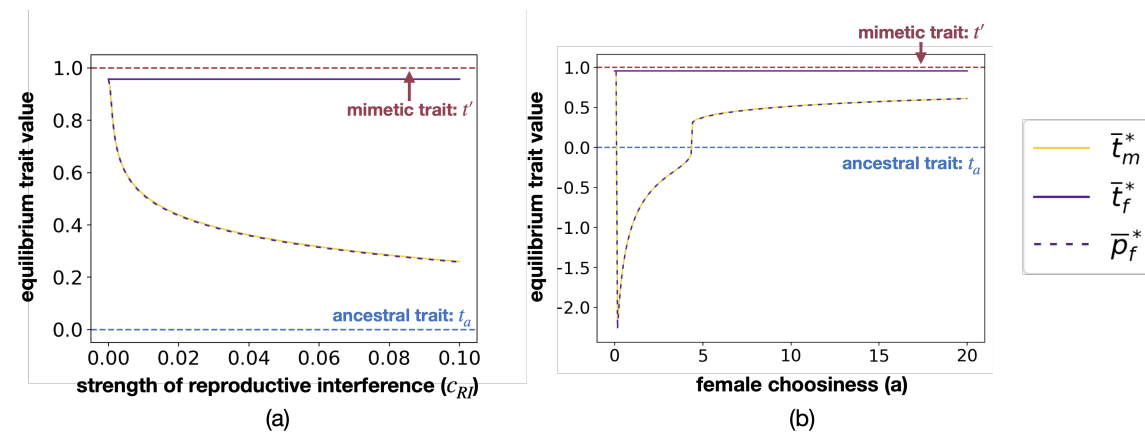

Figure 4: **Influence of (a) the strength of reproductive interference c_{RI} and (b) females choosiness a on the equilibrium values of males trait $\bar{t}_m^*$ (yellow solid line), females trait $\bar{t}_m^*$ (purple solid line) and females preference $\bar{p}_f^*$ (purple dashed line).** By default we assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $G_{t_m t_f} = 0.001$, $c_{RI} = 0.01$, $c = 0.1$, $a = 10$, $b = 5$, $d_m = d_f = 0.05$, $\lambda = 0$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.0025$, $t_a = 0$, $\bar{t}' = 1$.

We also investigate the impact of females choosiness (a) (modulating the stringency of sexual selection and cost of RI) on FLM, when there is RI ($c_{RI} > 0$) (Figure 4(b)). When a is close to 0, both males and females become mimetic to the *model* species (Figure 4(b)). In this case, non-choosy females tend to accept almost all males, despite their preference p_f. Thus selection on females preference p_f is low because a change on preference hardly changes the mating behaviour

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and the resulting cost of RI. When a is higher than 0 and approximately lower than 5, selection due to RI on preference is important and RI promotes FLM. Furthermore, our results show that sexual selection does not only inhibit mimicry in males but may further promote divergence away from the ancestral trait t_a (Figure 4(b), see Figure 2(b) for an illustration). Such divergence from the ancestral trait in males does not occur when females choosiness is higher ($a \gtrsim 5$ in Figure 4(b) see Figure 2(a) for an illustration): when females are more picky, a small difference between female preference and the mimetic trait sufficiently reduces the cost of RI (Figure 4(b)).

Sexually contrasted predation promotes female-limited mimicry in palatable species

Higher predation pressure acting on females has been proposed to explain FLM. Here we investigate the impact of the ratio of basal predation rate on males and females (d_m/d_f) on the evolution on FLM (Figure 5(a)) in case without RI and preference ($c_{RI} = 0, a = 0$). When predation pressures are largely lower in males than in females (*i.e.* $d_m/d_f \lesssim 0.2$), sexually contrasted predation promotes FLM (Figure 5(a)). Limited predation pressure in males implies low advantage to mimicry that is overcome by developmental constraints. By contrast, predation pressure is higher on females, resulting in a greater advantage to mimicry that overcomes costs of departure from ancestral trait value. However, when the predation ratio increases (*i.e.* $d_m/d_f \gtrsim 0.2$), sexual dimorphism is low, because advantage to mimicry in males becomes greater as compared to costs generated by developmental constraints (Figure 5(a)). When males and females suffer from similar predation pressure (*i.e.* $d_m/d_f = 1$), both sexes become mimetic (Figure 5(a)).
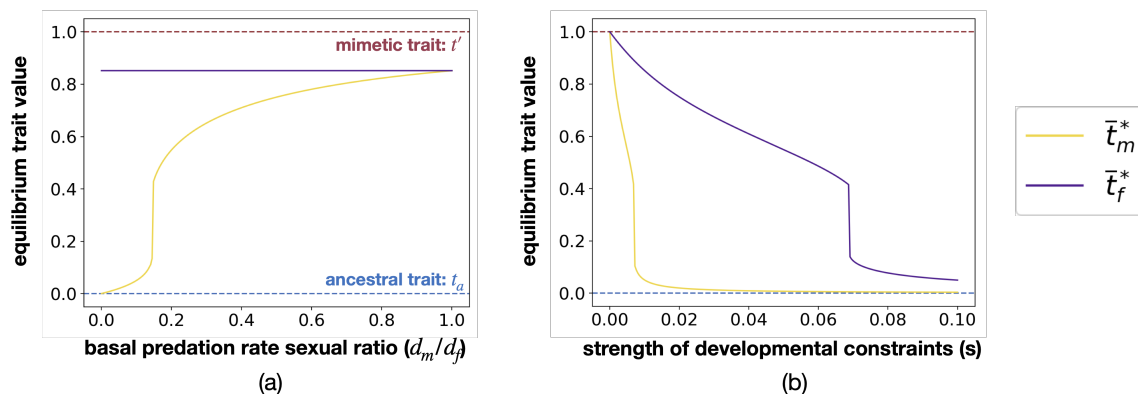

Figure 5: **Influence of (a) the ratio of basal predation rate on males and females (d_m/d_f) and (b) the strength of developmental constraints s on the equilibrium values of males trait $\bar{t}_m^*$ (yellow solid line), and females trait $\bar{t}_f^*$ (purple solid line).** By default we assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $G_{t_m t_f} = 0.001$, $c_{RI} = 0$, $c = 0.1$, $a = 0$, $b = 5$, $d_m = 0.05$, $d_f = 0.05$, $\lambda = 0$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.01$, $t_a = 0$, $\bar{t}' = 1$.

Because developmental constraints are a major factor limiting mimicry, we then investigate the impact of the strength of developmental constraints (s) on FLM generated by a sexually contrasted predation ($d_m/d_f = 0.1$). When there is no developmental constraints ($s = 0$), FLM does not evolve,

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because males become mimetic even if they suffer for low predation. However, higher developmental constraints ($0.1 \lesssim s \lesssim 0.7$) limit mimicry in males, but not in females because of sexually contrasted predation (see previous paragraph). Important developmental constraints ($s \gtrsim 0.7$) overcome the advantages provided by mimicry in both sexes, and prevent the evolution of sexual dimorphism.

Different hypothetical causes of female-limited mimicry lead to different predictions

Here, we use our mathematical model to compare the effect of (1) RI and (2) sexually contrasted predation on the evolution of FLM. We specifically investigate in which sex the trait evolves away from the ancestral trait, depending on the selective mechanism causing FLM.

First, we focus on the evolution of FLM caused by RI via sexual selection ($a > 0$ and $d_f = d_m$). We specifically estimate how (1) the distance between the ancestral trait and the mimetic trait $|t_a - t'|$ and (2) the female choosiness a modulate sexual selection and shape the relative divergence of males and females from the ancestral trait value $|\bar{t}_m^* - t_a| - |\bar{t}_f^* - t_a|$. Figure 6 highlights that divergence from the ancestral trait can be stronger in males (yellow zone on figure 6(a)) or in females (purple zone on Figure 6(a)) depending on these parameters.

The evolution of female trait only depends on the distance between the ancestral trait t_a and the mimetic trait t': because selection always promotes mimicry in females, divergence from the ancestral trait increases with the initial distance from the mimetic trait (Figure 6(c)). The level of mimicry in females slightly decreases with the ancestral level of mimicry because it increases the costs of developmental constraints. However, such costs are still overcame by the advantage of being mimetic. By contrast, the evolution of male trait depends on the interplay between the sexual selection generated by female preferences and the ancestral level of mimicry (Figure 6(b)).

When female choosiness is low (zone A, $a \lesssim 1.8$), the selection caused by RI is mild: not very choosy females tend to accept almost all males despite their preference p_f, therefore relaxing selection on females preference, and favouring the evolution of mimetic trait in males. Mimicry is nevertheless more accurate in females than in males, and males phenotype tends to stay closer to the ancestral trait value, and to display an "imperfect" mimicry. When the ancestral level of mimicry is poor ($|t_a - t'| \sim 1$), the slight advantage in sexual selection can then overcome the advantage of imperfect mimicry, resulting to divergence in males trait, even for low values of females choosiness ($a \lesssim 1.8$).

However, when females choosiness has intermediate values ($1.8 \lesssim a \lesssim 4$, zone B), enhanced female choosiness increases selection due to RI and thus reduces mimicry in males. Nevertheless, when the distance between the ancestral and the mimetic trait is already large, divergence in male trait is limited, and the sexual dimorphism mainly stems from the evolution of mimicry in females.

Contrastingly, high levels of choosiness in females ($a \gtrsim 4$, zone C) promote the evolution of more mimetic males because even a slight difference between the females preference and the mimetic trait allows to reduce cost of RI.Male divergence is then observed only when the ancestral level of resemblance between the *focal* and the *model* species is very high (*i.e* low $|t_a - t'|$), and therefore induced cost of RI, despite the high pickiness (*i.e.* high a) of females.

The evolution of FLM caused by RI therefore leads to different divergence patterns, including divergence of male phenotypes away from the ancestral trait value. In contrast when FLM is caused by sexually contrasted predation ($d_f > d_m$ and $a = 0$), sexual dimorphism always stems from the evolution of female phenotypes away from the ancestral trait, *i.e.* $|\bar{t}_f^* - t_a| > |\bar{t}_m^* - t_a|$ (see Appendix 6 and see Figure 2(a) for an illustration). While the two selective mechanisms may result in FLM,
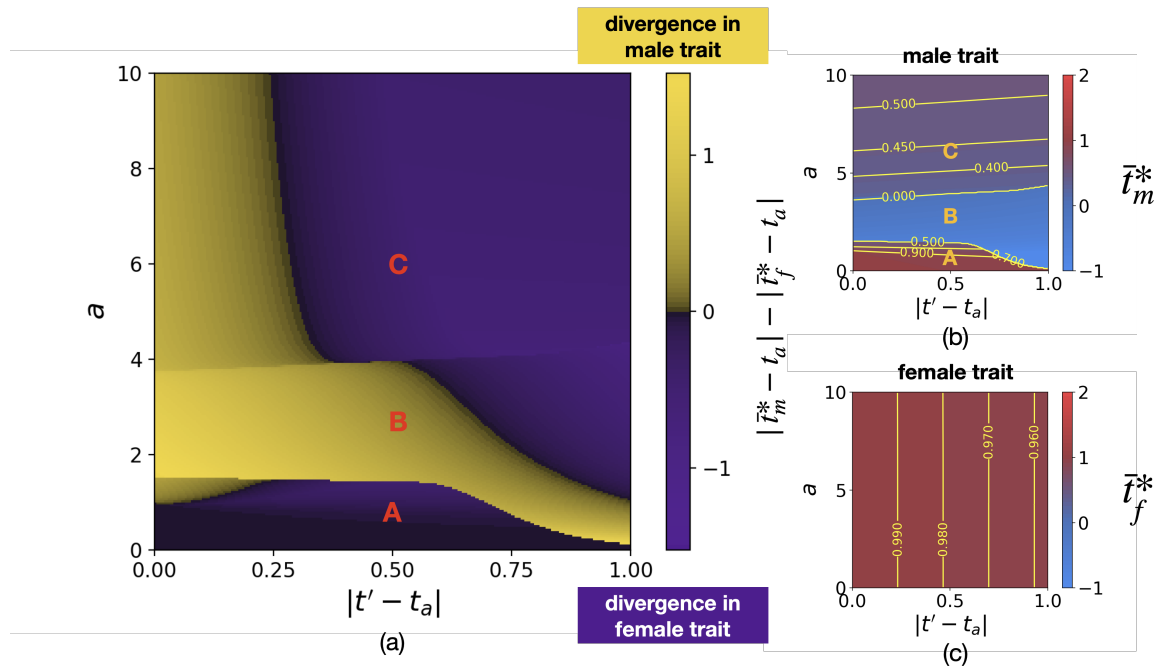
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Figure 6: **Influence of the distance between the ancestral and the mimetic traits** $|t' - t_a|$ **and of females choosiness** a **on (a) the difference between the level of divergence in males and females** $|\bar{t}_m^* - t_a| - |\bar{t}_f^* - t_a|$, **(b) final male trait** $\bar{t}_m^*$ **and (c) final female trait** $\bar{t}_f^*$. Yellow lines indicate equal levels of trait value. We assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $G_{t_m t_f} = 0.001$, $c_{RI} = 0.01$, $c = 0.1$, $b = 5$, $d_m = d_f = 0.05$, $\lambda = 0$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.0025$, $t_a = 0$.

the evolutionary pathways causing the sexual dimorphism are thus strikingly different.

The evolution of FLM depends on defence level

We then investigate the impact of the individual defence level (λ) and the density (N) in the *focal* species on the evolution of sexual dimorphism, when FLM is generated either (1) by sexually contrasted predation (Figure 7) or (2) by RI via sexual selection (Figure 8).

Surprisingly, when FLM is caused by sexually contrasted predation $(d_f > d_m)$, the level of sexual dimorphism first increases with defence levels in both males and females $(\lambda N/2)$ (Figure 7(a)). In both sexes, the increase in defence levels indeed reduces selection favouring mimicry, while the developmental and selective constraints favour ancestral trait value. Moreover, the more limited predation pressure exerted on males further impairs convergent evolution towards mimetic trait in males (Figure 7(b)). In this range of mild levels of defence, mimicry is nevertheless advantageous in heavily-attacked females (Figure 7(c)), resulting in high level of sexual dimorphism. However, when the defence level becomes very high, both males and females display the ancestral trait, and sexual dimorphism is no longer observed (Figure 7(b) and (c) at the top right). Because of the
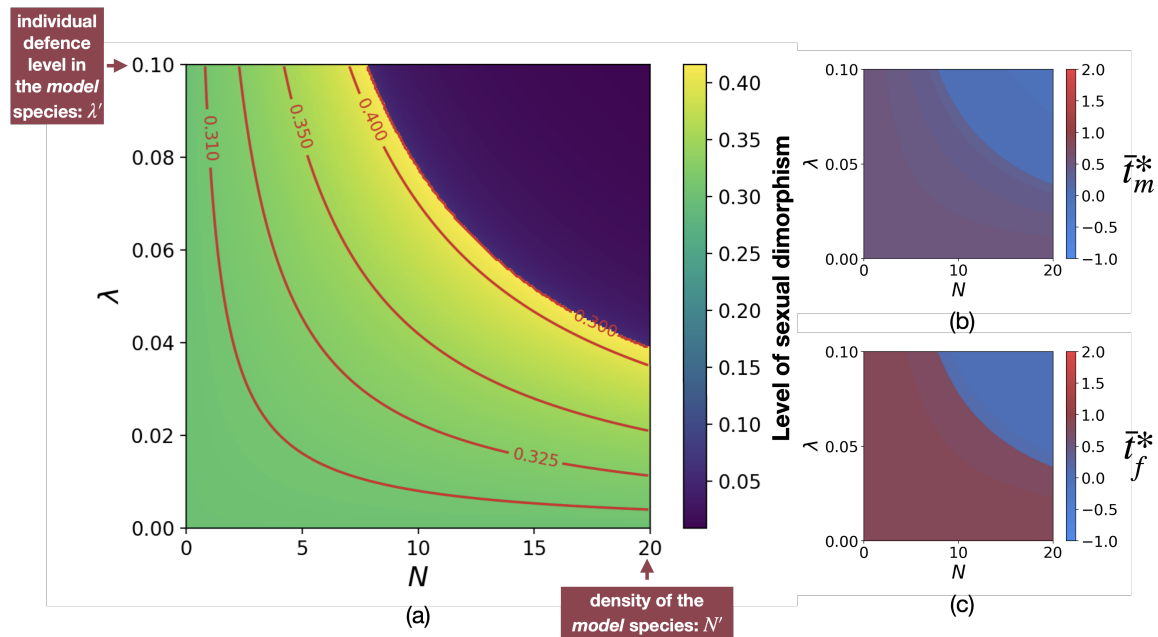
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Figure 7: **Influence of the density N and of the individual defence level λ in the *focal* species on the equilibrium values of (a) the level of sexual dimorphism ($|\bar{t}_m^* - \bar{t}_f^*|$), (b) males trait $\bar{t}_m^*$ and (c) females trait $\bar{t}_f^*$ when female-limited mimicry is caused by sexually contrasted predation ($d_f > d_m$, $a = 0$).** Red lines indicate equal levels of sexual dimorphism. We assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $G_{t_m t_f} = 0.001$, $c_{RI} = 0$, $c = 0.1$, $a = 0$, $b = 5$, $d_m = 0.01$, $d_f = 0.05$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.01$, $t_a = 0$, t'.

high level of defence, individuals of both sexes gain sufficient protection from similarity with their conspecifics, relaxing selection promoting mimicry towards the *model* species.

Similarly, when FLM is caused by RI ($c_{RI} > 0$) via sexual selection, the level of sexual dimorphism also increases with the individual defence level λ, because the advantages of mimicry decrease when the individuals of the *focal* species are well-defended. Increased defences indeed particularly decrease convergence towards the *model* species in males submitted to divergent sexual selection. In contrast with predation differences between sexes, sexual selection induced by RI makes sexual dimorphism higher for low values of density of the *focal* species ($N < \frac{N'}{2}$) (Figure 8(a)). The relative density of the *focal* and the *model* species determines the probability that a female of the *focal* species encounters a conspecific rather than an heterospecific male and thus also modulates the costs of RI. Therefore, when the density of the *focal* species N is low, costs of RI are great, generating higher sexual dimorphism.

Surprisingly when the individual defence level is high ($\lambda \simeq 0.1$) sexual dimorphism increases with the density of the *focal* species (Figure 8(a)). In this case, RI barely impacts males trait: the high defence level in males promotes trait sufficiently close to the ancestral trait that females easily distinguish between conspecific and heterospecific males. Therefore an increase of density
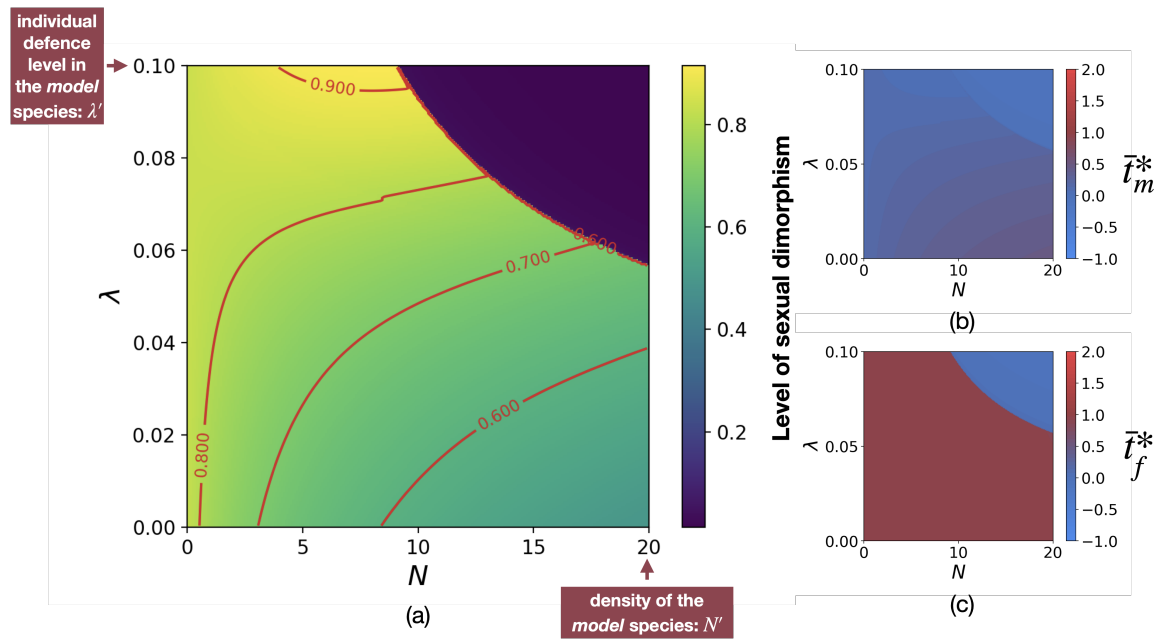
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(a)

(b)

(c)

Figure 8: **Influence of the density N and of the individual defence level λ in the *focal* species on the equilibrium values of (a) the level of sexual dimorphism $|\bar{t}_m^* - \bar{t}_f^*|$, (b) males trait $\bar{t}_m^*$ and (c) females trait $\bar{t}_f^*$ when female-limited mimicry is generated by sexual selection caused by RI (c_{RI}, $a > 0$ and $d_f = d_m$).** Red lines indicate equal levels of sexual dimorphism. We assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $G_{t_m t_f} = 0.001$, $c_{RI} = 0.01$, $c = 0.1$, $a = 5$, $b = 5$, $d_m = d_f = 0.05$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.0025$, $t_a = 0$, t'.

increases defence level without reducing cost of RI that is already low. However when RI is strong
460   enough and promotes a higher phenotypic distance between conspecific and heteropspcific males
than ancestrally, the level of sexual dimorphism is always maximum when the density is low (see
462   Appendix 7).

Under both hypotheses explaining female limited-mimicry, when the level of defence in the
464   mimetic species is low (*i.e.* in quasi-Batesian mimics), sexual dimorphism is predicted to increase
with the level of defence. In the same range of defence values (*i.e.* in quasi-Batesian mimics), under
466   the assumption of sexual selection generated by RI however, sexual dimorphism is generally higher
when the *focal* species is rarer than the *model* species.

468   Under both selective hypotheses, FLM is no longer promoted when the level of defence within the
focal species is high.

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Discussion

Ancestral levels of resemblance, sexually-contrasted divergences and the evolution of female-limited mimicry

Our model highlights that both (1) sexually contrasted predation and (2) females preference generated by RI can favour the evolution of FLM. By explicitly studying how these contrasted selective pressures influence the divergence of males and females traits from a common ancestral trait, our model sheds light on contrasted evolutionary pathways towards sexual dimorphism. Empirical studies based on the estimation of the level of divergence in males and females traits usually interpret elevated divergence in males trait as compared to female trait, as a signature of sexual selection, causing sexual dimorphism [van der Bijl et al., 2020]. Focusing on FLM in *Papilio* butterflies, Kunte [2008] shows that sexual dimorphism is correlated with divergence in females trait, and concluded that FLM is caused by natural selection. However, our results show that when RI induces females preference, FLM can also stem from an increased divergence in female trait. Our results therefore highlight that higher divergence in female trait is not a reliable evidence of sexually-contrasted selection promoting FLM.

Our model highlights that depending on the ancestral level of phenotypic resemblance between currently mimetic species, the divergence of males traits caused by females preference might differ. Our results thus stress the need to account for ancestral levels of mimicry and to consider the effect of RI when investigating the evolutionary causes of FLM.

The level of investment of males in reproduction and the evolution of FLM caused by RI

Our results show that RI can generate females preference for non-mimetic males and therefore may cause FLM. Some studies already suggested that sexual selection may generate FLM [Belt, 1874., Turner, 1978], but the origin of females preferences for non-mimetic males was unidentified. Our model highlights that RI could be the driver of such females preferences.

Nevertheless, the emergence of sexual dimorphism stems from the assumption that female is the only choosy sex. This assumption is relevant when females invest much more in reproduction than males [Trivers, 1972, Balshine et al., 2002]. However, this asymmetrical investment in offspring between males and females can vary in different Lepidoptera species. Butterfly males frequently provide a nuptial gift containing nutriments during mating [Boggs and Gilbert, 1979]. Such elevated cost of mating in males could promote the evolution of choosiness in males. If the asymmetry in reproductive investment between sexes is limited, the evolution of FLM would then be impaired. Moreover, the investment of males in reproduction impacts the cost of choosiness for females, because females refusing a mating opportunity would be denied access to the nuptial gift. In Lepidoptera females mating more that once have higher lifetime fecundity than females that mate only once, because nuptial gifts provide important metabolic resources [Wiklund et al., 1993, Lamunyon, 1997]. Such elevated cost of rejecting a potential mate may limit the evolution of preference in females, as highlighted by our model: our results indeed show that RI promotes FLM only when cost of choosiness is low. The evolution of female-mimicry is thus likely to be impaired when the costs of mating are elevated in males, and therefore (1) inducing male choosiness and (2) increasing the opportunity costs generated by female choosiness. Experimental approaches estimating the reproductive costs and benefits in both sexes are thus crucially needed to understand

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512   the evolution of FLM caused by RI.

Relative species abundances and defences and the evolution of female-limited mimicry

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Our results show that, for both causes of FLM (RI or sexually contrasted predation), the level of
516   sexual dimorphism increases with the individual level of defence. This prediction appears in sharp
discrepancy with the empirical observation reporting FLM mostly in Batesian mimics, although
518   FLM has still been reported in a few defended species [Nishida, 2017]. Our model stresses the
need to precisely quantify the level of defences carried out by individuals from different species:
520   important variations in the levels of defences within species have been documented in Müllerian
mimics (*e.g.* in *Heliconius* butterflies, Sculfort et al. [2020]), as well as in Batesian mimics (*e.g.*
522   viceroy butterfly, Prudic et al. [2019]). Empirical quantification of the level of deterrence induced
by individuals from co-mimetic species would shed light on the evolutionary conditions favouring
524   the evolution of FLM.

526   Our model also predicts that the emergence of FLM is strongly linked to the relative density
between mimics and models, and our theoretical approach neglects the dynamics of population
528   densities of the *focal* and the *model* species, that may depend on their individual defence level.
Empirical studies usually report that the density of undefended mimics is low compared to those
530   of the defended models [Long et al., 2015, Prusa and Hill, 2021]. Undefended mimics can have a
negative effect predator's learning [Rowland et al., 2010, Lindström et al., 1997], suggesting that
532   Batesian mimicry could evolve and be maintained only in species with a low density compared to
the *model* species. Moreover, a high abundance of the *model* species compared to the potential
534   mimics also increases the protection of imperfect mimics allowing the evolution of gradual Batesian
mimicry [Kikuchi and Pfennig, 2010]. The relative density between the *focal* and the *model* species
536   is especially important when assuming RI, because the costs generated by heterospecific interactions
depend on the proportion of heterospecific males encountered by females. Our results show that RI
538   strongly promotes sexual dimorphism when the density of the *focal* species in low as compared to
the *model* species. Considering that FLM is caused by RI, the lower relative density of undefended
540   species may promote FLM, and therefore explain why FLM could be especially favoured in Batesian
mimics is reserved to undefended species.
542   The reported difference in phenology between defended *models* emerging sooner than undefended
mimics may further enhance the difference in relative abundances between *models* and *mimics*,
544   therefore increasing the cost of RI for undefended females. Batesian mimics often emerge after
their models, when the models warning signal is well known by predators [Prusa and Hill, 2021],
546   and this might reinforce the evolution of FLM caused by RI in Batesian *mimics*.

Conclusion

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Our model show that both sexually contrasted predation and RI (by promoting preference for non-
550   mimetic males) may generate FLM. Our results therefore show that the patterns of divergence of
males and females traits from ancestral state should be interpreted in light from the selection regime
552   involved. Our model also reveals the important role of ecological interactions between sympatric

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species on the evolution of sexual dimorphism, highlighting the need to consider the role of eco-evolutionary feedbacks in the phenotypic diversification in sympatry.

Acknowledgments

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Appendix

1   Selection vectors

In this part we detail the calculations to obtain the selection vector (Equation (2)).

1.1   Selection acting on males trait β_{t_m}

We compute the first component of the selection vector β_{t_m} describing the selection acting on males trait. This coefficient is given by

$$\beta_{t_m} = \frac{d}{dt_m} \log\left(W(t_m, t_f, p_f)\right)\bigg|_{(t_m, t_f, p_f)=(\bar{t}_m, \bar{t}_f, \bar{p}_f)}.$$

Using (1) and (6) we have

$$\beta_{t_m} = -2s(\bar{t}_m - t_a) + \frac{d}{dt_m} \log\left(W^{\male}_{pred}(t_m)\right)\bigg|_{t_m=\bar{t}_m} + \frac{d}{dt_m} \log\left(W_r(t_m, p_f)\right)\bigg|_{(t_m, p_f)=(\bar{t}_m, \bar{p}_f)}.$$

1.1.1   Selection due to predation

First we compute the part of the selection coefficient due to predation. Using (10) we have:

$$\frac{d}{dt_m} \log\left(W^{\male}_{pred}(t_m)\right)\bigg|_{t_m=\bar{t}_m} = \frac{d}{dt_m}\left(\frac{-d_m}{1+\mathcal{D}(t_m)}\right)\bigg|_{t_m=\bar{t}_m},$$

$$= \left(\frac{d_m \frac{d}{dt_m}\mathcal{D}(t_m)}{(1+\mathcal{D}(t_m))^2}\right)\bigg|_{t_m=\bar{t}_m}.$$

Using (9) we have

$$\frac{d}{dt}\mathcal{D}(t) = -b(t-\bar{t}_m)\lambda N \exp\left[-b(t-\bar{t}_m)^2\right] - b(t-\bar{t}_f)\lambda N \exp\left[-b(t-\bar{t}_f)^2\right]$$

$$- 2b(t-\bar{t}')\lambda' N' \exp\left[-b(t-\bar{t}')^2\right].$$

1.1.2   Selection due to reproduction

We now compute the part of the selection coefficient due to reproduction. Using (21) we have:

$$\frac{d}{dt_m} \log\left(W_r(t_m, p_f)\right)\bigg|_{(t_m, p_f)=(\bar{t}_m, \bar{p}_f)} = -2a(\bar{t}_m - \bar{p}_f).$$

Therefore we have

$$\beta_{t_m} = -2s(\bar{t}_m - t_a) + \frac{d_m \frac{d}{dt_m}\mathcal{D}(t_m)\big|_{t_m=\bar{t}_m}}{(1+\mathcal{D}(\bar{t}_m))^2} - 2a(\bar{t}_m - \bar{p}_f).$$

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1.2 Selection acting on females trait β_{t_f}

The second component of the selection vector β_{t_f} is given by

$$\beta_{t_f} = \frac{d}{dt_f} \log\left(W(t_m, t_f, p_f)\right)\Big|_{(t_m, t_f, p_f)=(\bar{t}_m, \bar{t}_f, \bar{p}_f)}.$$

Using (1) and (7) we have

$$\beta_{t_f} = -2s(\bar{t}_f - t_a) + \frac{d}{dt_f} \log\left(W^{\female}_{pred}(t_f)\right)\Big|_{t_f=\bar{t}_f}.$$

Similarly than with male traits we have

$$\frac{d}{dt_f} \log\left(W^{\female}_{pred}(t_f)\right)\Big|_{t_f=\bar{t}_f} = \left(\frac{d_f \frac{d}{dt_f} \mathcal{D}(t_f)}{(1 + \mathcal{D}(t_f))^2}\right)\Big|_{t_f=\bar{t}_f}.$$

Thus we have

$$\beta_{t_f} = -2s(\bar{t}_f - t_a) + \frac{d_f \frac{d}{dt_f} \mathcal{D}(t_f)\Big|_{t_f=\bar{t}_f}}{(1 + \mathcal{D}(\bar{t}_f))^2}.$$

1.3 Selection acting on females preference β_{p_f}

The last component of the selection vector β_{t_f} is given by

$$\beta_{p_f} = \frac{d}{dp_f} \log\left(W(t_m, t_f, p_f)\right)\Big|_{(t_m, t_f, p_f)=(\bar{t}_m, \bar{t}_f, \bar{p}_f)}.$$

Using (1) we have

$$\beta_{p_f} = \frac{d}{dp_f} \log\left(W_r(t_m, p_f)\right)\Big|_{(t_m, p_f)=(\bar{t}_m, \bar{p}_f)}.$$

Using (21) we have

$$\beta_{p_f} = \frac{d}{dp_f} \log\left(T(p_f)\right)\Big|_{p_f=\bar{p}_f}$$
$$- \frac{d}{dp_f} \log\left(c + (1-c)(T(p_f) + T_{RI}(p_f))\right) - 2a(p_f - t_m) + 2a(p_f - \bar{t}_m)\Big|_{(t_m, p_f)=(\bar{t}_m, \bar{p}_f)}.$$

Using (15) and (16) we have

$$\frac{d}{dp_f} \log\left(T(p_f)\right)\Big|_{p_f=\bar{p}_f} = -2a(\bar{p}_f - \bar{t}_m),$$

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and

$$\frac{d}{dp_f} \log\left(c + (1-c)(T(p_f) + T_{RI}(p_f))\right)\bigg|_{p_f = \overline{p}_f}$$

$$= \frac{(1-c)\left(-2a(\overline{p}_f - \overline{t}_m)T(\overline{p}_f) - 2a(\overline{p}_f - \overline{t}')T_{RI}(\overline{p}_f)\right)}{c + (1-c)(T(\overline{p}_f) + T_{RI}(\overline{p}_f))}.$$

Thus

$$\beta_{p_f} = -2a(\overline{p}_f - \overline{t}_m)$$

$$+ 2a\frac{(1-c)\left((\overline{p}_f - \overline{t}_m)T(\overline{p}_f) + (\overline{p}_f - \overline{t}')T_{RI}(\overline{p}_f)\right)}{c + (1-c)(T(\overline{p}_f) + T_{RI}(\overline{p}_f))}.$$

2 Computation of the matrix of correlation

In this part we approximate the genetic covariance between males trait and females preference $G_{t_m p_f}$, using the results from [Kirkpatrick et al., 2002]. Trait and preference are controled by different sets of unlinked loci with additive effects, denoted T and P, respectively. We note $T_m \subseteq T$ and $T_f \subseteq T$ the loci controlling trait in males and in females respectively. For each i in T (resp. P), we note ξ_i^t (resp. ξ_i^p) the contribution of the locus i on trait (resp. preference) value. The trait t_m of a male is then given by

$$t_m = \sum_{i \in T_m} \xi_i^t. \tag{A1}$$

The trait t_f and preference p_f values of a female are given by

$$t_f = \sum_{i \in T_f} \xi_i^t \quad \text{and} \quad p_f = \sum_{i \in P} \xi_i^p. \tag{A2}$$

As in [Lande, 1981] we assume that the distributions of ξ_i^t and ξ_i^p are multivariate Gaussian. Let G_{ij} be the genetic covariance between loci i and j. Then the elements of the matrix of correlation are given by:

$$G_{t_m t_m} = \sum_{i,j \in T_m} G_{ij}, \quad G_{t_f t_f} = \sum_{i,j \in T_f} G_{ij}, \quad G_{p_f p_f} = \sum_{i,j \in P} G_{ij} \quad \text{and} \quad G_{t_m p_f} = \sum_{i \in T_m, j \in P} G_{ij}. \tag{A3}$$

To compute the change on genetic correlation we need to identify various selection coefficients (see [Barton and Turelli, 1991, Kirkpatrick et al., 2002]). These coefficients are obtained using the contribution to the next generation of a mating between a male with trait t_m and a female with trait t_f and preference p_f due to natural selection and mating preference (see equation 1).

For simplicity we consider only leading terms in the change in genetic correlation, computed with a Mathematica script (available online at https://github.com/Ludovic-Maisonneuve/evo-flm).

For $(i,j) \in T_m \times P_f$, combining Equations (9), (12), (15) from Kirkpatrick et al. [2002] gives the change in the genetic covariance between loci i and j:

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$$\Delta G_{ij} = -\frac{G_{ij}}{2} + \frac{1}{4}\tilde{a}_{t_m t_m} \sum_{k,l \in T_m} (G_{ik}G_{jl} + G_{il}G_{jk}) + \frac{1}{4}\tilde{a}_{p_f p_f} \sum_{k,l \in P} (G_{ik}G_{jl} + G_{il}G_{jk})$$

$$+ \frac{1}{4}\tilde{a}_{t_m p_f} \sum_{k \in T_m, l \in P} G_{ik}G_{jl} + \frac{1}{4}\tilde{a}_{t_m p_f} \sum_{k \in T_m, l \in P} G_{il}G_{jlk} + O(\varepsilon^2) \tag{A4}$$

with $\tilde{a}_{\mu\rho}$ for $(\mu,\rho) \in \{t_m, t_f, p_f\}^2$ being the leading term of the selection coefficients $a_{\mu\rho}$ calculated from the contribution to the next generation:

$$a_{\mu\rho} := \frac{1}{2} \frac{\partial^2}{\partial\mu\partial\rho} \log(W(t_m, t_f, p_f)) \bigg|_{(t_m, t_f, p_f) = (\bar{t}_m, \bar{t}_f, \bar{p}_f)} .$$

We obtain

$$\tilde{a}_{p_f p_f} = -\frac{ac(N + N')}{N + cN'},$$

$$\tilde{a}_{t_m t_m} = -a,$$

and

$$\tilde{a}_{t_m p_f} = 2a.$$

By summing Equations (A4) over each i, j in T_m and P we obtain:

$$\Delta G_{t_m p_f} = -\frac{G_{t_m p_f}}{2} - \frac{1}{2}aG_{t_m t_m}G_{t_m p_f} - \frac{1}{2}\frac{ac(N + N')}{N + cN'}G_{p_f p_f}G_{t_m p_f}$$

$$+ \frac{1}{2}aG_{t_m t_m}G_{p_f p_f} + \frac{1}{2}aG_{t_m p_f}^2 + O(\varepsilon^2). \tag{A5}$$

Under weak selection genetic correlations quickly reach equilibrium [Nagylaki, 1993]. For the sake of simplicity we assumed that the genetic correlations between traits and preferences are at equilibrium (as in [Barton and Turelli, 1991, Pomiankowski and Iwasa, 1993]). We obtain from (A5) that the two possible values at equilibrium are given by

$$\frac{1}{2a}\left(1 + aG_{t_m t_m} + \frac{acG_{p_f p_f}(N + N')}{N + cN'}\right.$$

$$\left. \pm \sqrt{\left(1 + aG_{t_m t_m} + \frac{acG_{p_f p_f}(N + N')}{N + cN'}\right) - 4a^2 G_{p_f p_f}G_{t_m t_m}}\right).$$

Only one of the two equilibrium values checks the Cauchy–Schwarz inequality ($G_{t_m p_f} \leq \sqrt{G_{t_m t_m}G_{p_f p_f}}$). Therefore the equilibrium value is given by:

$$G_{t_m p_f}^* = \frac{1}{2a}\left(1 + aG_{t_m t_m} + \frac{acG_{p_f p_f}(N + N')}{N + cN'}\right. \tag{A6}$$

$$\left. \pm \sqrt{\left(1 + aG_{t_m t_m} + \frac{acG_{p_f p_f}(N + N')}{N + cN'}\right) - 4a^2 G_{p_f p_f}G_{t_m t_m}}\right).$$

Because the genetic variance of traits and preferences is low, a Taylor expansion of (A6) gives

$$G^*_{t_m p_f} \approx a G_{t_m t_m} G_{p_f p_f}.$$

3   Low variance approximation

Because we assume that the variance of traits and preference is low we may use approximation in Equations (9), (15), (16) and (18). Here we detail how we obtained these approximations. The reasoning is similar for each approximation so we only explain how we get an approximation of $\mathcal{D}$ in (9). We recall that $\mathcal{D}$ is defined by

$$\mathcal{D}(t) = \int_{\tau_m} \lambda \frac{N}{2} f^{\male}(\tau_m) \exp\left[-b(t-\tau_m)^2\right] \mathrm{d}\tau_m + \int_{\tau_f} \lambda \frac{N}{2} f^{\female}(\tau_f) \exp\left[-b(t-\tau_f)^2\right] \mathrm{d}\tau_f$$

$$+ \int_{t'} \lambda' N' g(t') \exp\left[-b(t-t')^2\right] \mathrm{d}t'.$$

We first approximate the first term of $\mathcal{D}$. We have

$$\int_{\tau_m} \lambda \frac{N}{2} f^{\male}(\tau_m) \exp\left[-b(t-\tau_m)^2\right] \mathrm{d}\tau_m$$

$$= \lambda \frac{N}{2} \exp\left[-b(t-\bar{t}_m)^2\right] \int_{\tau_m} f^{\male}(\tau_m) \exp\left[b(2t-\tau_m-\bar{t}_m)(\tau_m-\bar{t}_m)\right] \mathrm{d}\tau_m.$$

Using a Taylor expansion of $\exp\left[b(2t-\tau_m-\bar{t}_m)(\tau_m-\bar{t}_m)\right]$ we have

$$\lambda \frac{N}{2} \exp\left[-b(t-\bar{t}_m)^2\right] \int_{\tau_m} f^{\male}(\tau_m) \left(1 + b(2t-\tau_m-\bar{t}_m)(\tau_m-\bar{t}_m) + O((\tau_m-\bar{t}_m)^2)\right) \mathrm{d}\tau_m,$$

which is equal to

$$\lambda \frac{N}{2} \exp\left[-b(t-\bar{t}_m)^2\right] \left(1 - b\mathrm{Var}(t_m) + O(\mathrm{Var}(t_m))\right).$$

Hence when the variance of t_m is low the first term of $\mathcal{D}$ can be approximated by

$$\lambda \frac{N}{2} \exp\left[-b(t-\bar{t}_m)^2\right].$$

Similar computations for the other terms give the approximation in Equation (9).

4 RI promotes female-limited mimicry in palatable species when females have sufficiently low cost of choosiness

The evolution of FLM strongly depends on the evolution of females preference. As we have already seen the evolution of females preference depends on RI promoting preferences for non-mimetic males. However such preferences may cause females to seek for rarer males in the population. The evolution of preference limiting the cost of RI may thus be limited by the cost of choosiness described by the parameter c. We thus investigate the impact of the strength of RI (c_{RI}) promoting FLM and the cost of choosiness (c) on the final level of sexual dimorphism given by $|\bar{t}_m^* - \bar{t}_f^*|$ (Figure A1 (a)) and on final females preference $\bar{p}_f^*$ (Figure A1 (b)). Cost of choosiness limits the evolution of sexual dimorphism due to RI (Figure A1 (a)) because it limits the evolution of females preference (Figure A1 (b)). In natural population, RI may explain FLM in populations where females have low cost of choosiness.
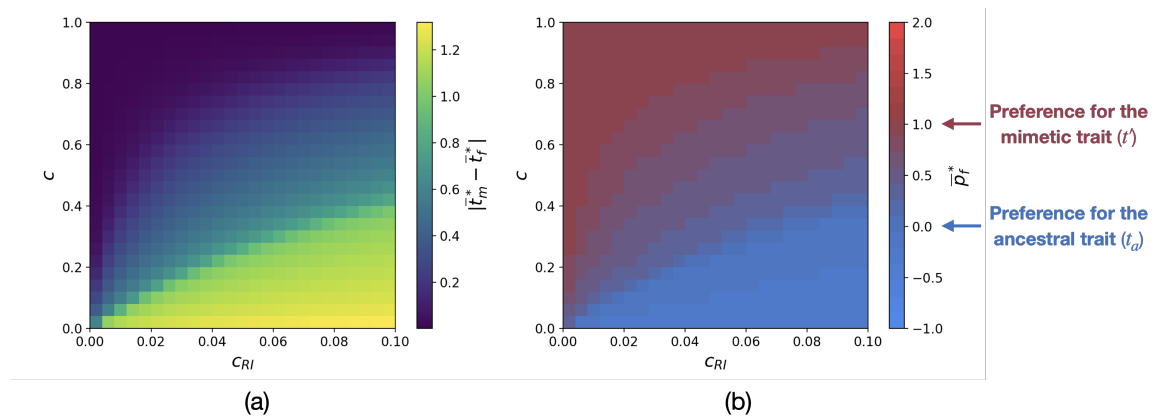

Figure A1: **Influence of the strength of reproductive interference c_{RI} and of the cost of choosiness c on the final level of sexual dimorphism $|\bar{t}_m^* - \bar{t}_f^*|$ and final preference $\bar{p}_f^*$.** We assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $G_{t_m t_f} = 0.001$, $a = 5$, $b = 5$, $d_m = d_f = 0.05$, $\lambda = 0$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.0025$, $t_a = 0$, $\bar{t}' = 1$.

5 Impact of the genetic correlation between males and females traits $C_{t_m t_f}$

The evolution of the mean males and females trait values ($\bar{t}_m$ and $\bar{t}_f$) depends on the genetic covariance between males and females traits ($G_{t_m t_f}$) (see equation (2)). We investigate the impact of this genetic covariance and of the strength of RI (c_{RI}) on the level of sexual dimorphism (Figure A2). The level of sexual dimorphism is not impacted by the genetic covariance unless this quantity is at its maximum value ($G_{t_m t_f} = \sqrt{G_{t_m t_m} G_{t_f t_f}}$). Indeed when the genetic covariance is at it maximum value males and females traits have the same genetic basis, therefore the evolution of sexual dimorphism is not possible. By contrast when males and females traits have at least partially different genetic basis ($G_{t_m t_f} < \sqrt{G_{t_m t_m} G_{t_f t_f}}$) the non-shared genetic basis allows the level of sexual dimorphism to increase.
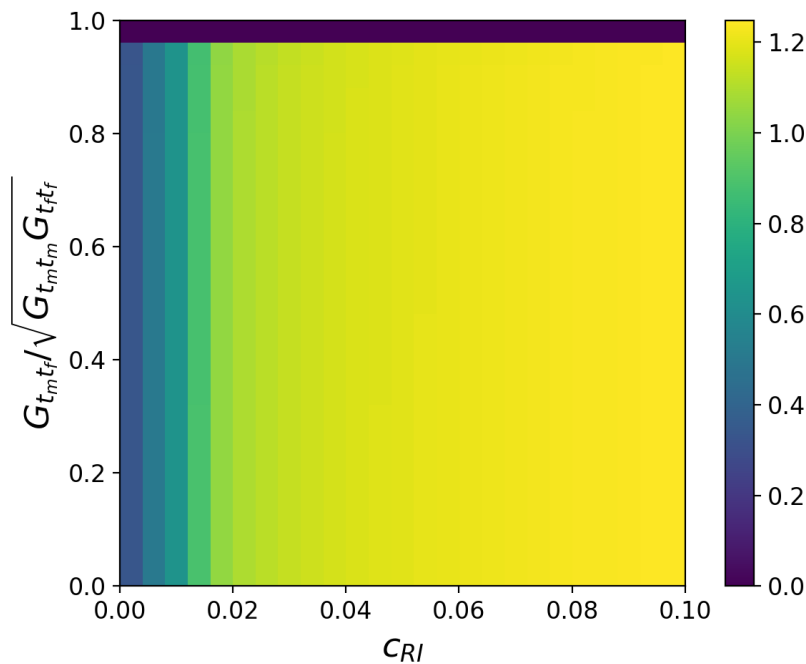

Figure A2: **Influence of the strength of reproductive interference c_{RI} and of the genetic covariance between males and females traits normalized by its maximum value** $\frac{G_{t_m t_f}}{\sqrt{G_{t_m t_m} G_{t_f t_f}}}$ **on the final level of sexual dimorphism** $|\bar{t}_m^* - \bar{t}_f^*|$. We assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $c = 0.1$, $a = 5$, $b = 5$, $d_m = d_f = 0.05$, $\lambda = 0$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.0025$, $t_a = 0$, $\bar{t}' = 1$.

However $G_{t_m t_f}$ impacts the speed at which the equilibrium is reached. When males trait in the *focal* species gets closer to the mimetic trait the genetic correlation increases the speed of convergence because selection on females trait also favours mimicry and also acts on males trait. By contrast when males trait diverges away from the mimetic trait the genetic correlation decreases

912   the speed of convergence.

(a)   (b)   (c)

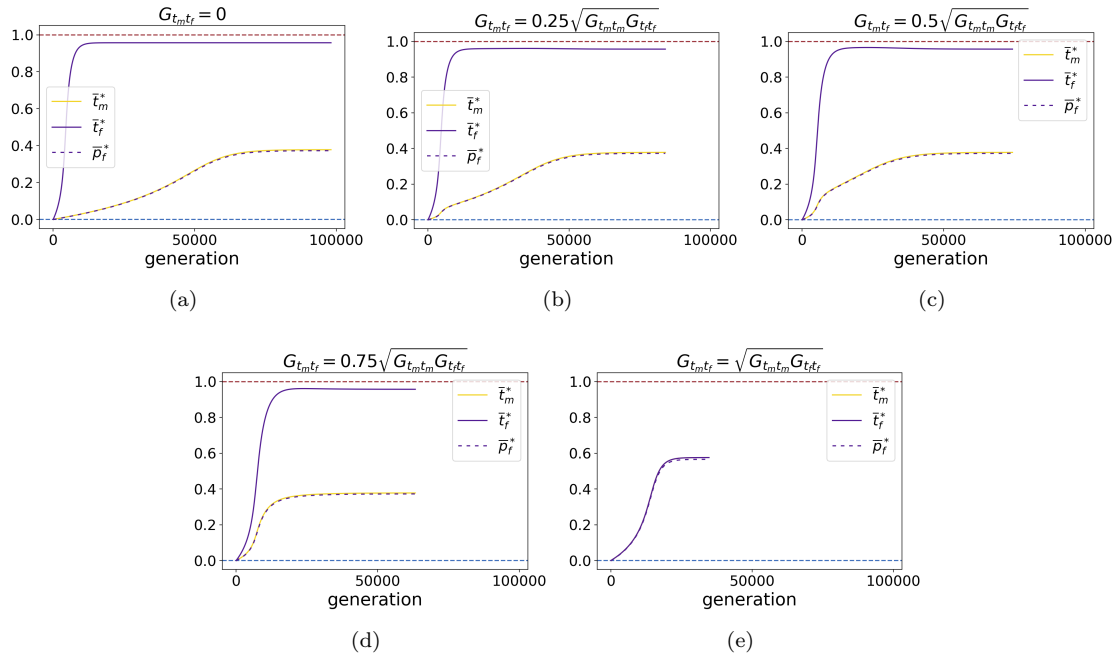(d)   (e)

Figure A3: **Evolution of the mean males trait and females trait and preference values across generations for different genetic covariances between males and females traits** $G_{t_m t_f}$ **when males trait gets closer to the mimetic trait.** We assume different values of the genetic covariance between male and female traits: (a) $G_{t_m t_f} = 0$, (b) $G_{t_m t_f} = 0.25\sqrt{G_{t_m t_m} G_{t_f t_f}}$, (c) $G_{t_m t_f} = 0.5\sqrt{G_{t_m t_m} G_{t_f t_f}}$, (d) $G_{t_m t_f} = 0.75\sqrt{G_{t_m t_m} G_{t_f t_f}}$, (e) $G_{t_m t_f} = \sqrt{G_{t_m t_m} G_{t_f t_f}}$. We assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $G_{t_m t_f} = 0.001$, $c_{RI} = 0.01$, $c = 0.1$, $a = 5$, $b = 5$, $d_m = d_f = 0.05$, $\lambda = 0$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.0025$, $t_a = 0$, $\bar{t}' = 1$. The curves stop when the males trait and females trait and preference values reach equilibrium.

6   Sexually contrasted predation promotes higher trait di-
914   vergence in females

In this part we show that if FLM in a palatable species ($\lambda = 0$) is not caused by sexual selection
916   ($a = 0$) but by sexually contrasted predation ($d_f > d_m$) then at the final state females trait ($\bar{t}_f^*$)
diverges more from the ancestral trait than male trait ($\bar{t}_m^*$). In mathematical terms we prove that
918   if $a = 0$ and $d_f > d_m$ we have

920
$$|\bar{t}_f^* - t_a| > |\bar{t}_m^* - t_a|. \tag{A7}$$

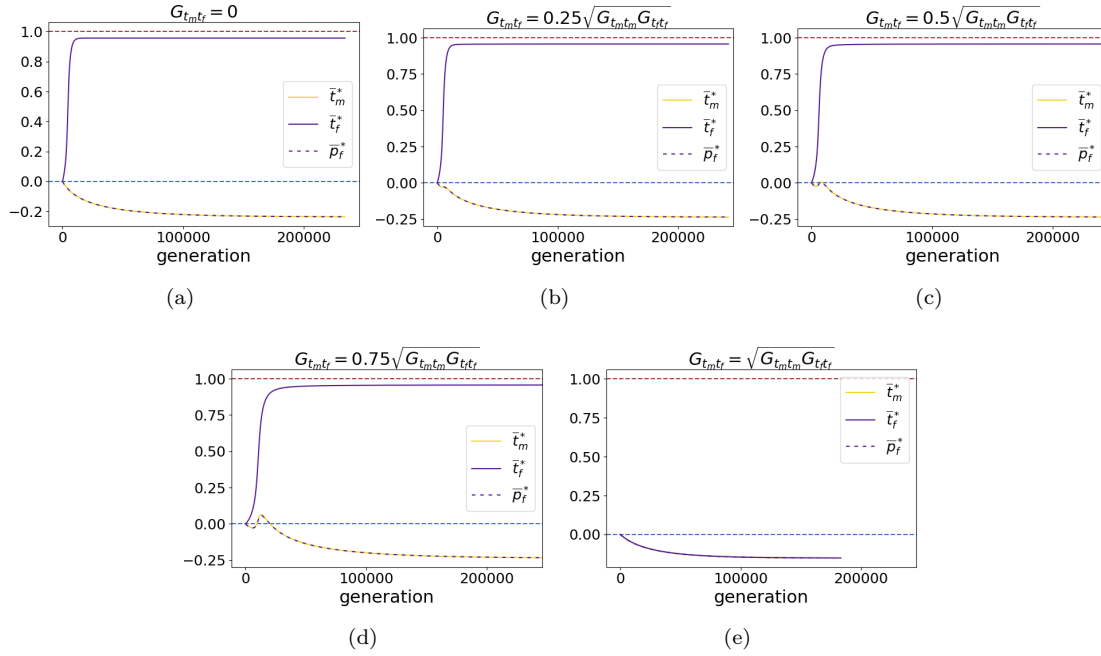For simplicity we assume that $t' > t_a$, the other case being obtained by symmetry.

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Figure A4: **Evolution of the mean males trait and females trait and preference values across generations for different genetic covariances between male and female traits** $G_{t_m t_f}$ **when reproductive interference promotes divergence of males trait away from the mimetic trait.** We assume different value of the genetic covariance between of male and female trait: (a) $G_{t_m t_f} = 0$, (b) $G_{t_m t_f} = 0.25\sqrt{G_{t_m t_m} G_{t_f t_f}}$, (c) $G_{t_m t_f} = 0.5\sqrt{G_{t_m t_m} G_{t_f t_f}}$, (d) $G_{t_m t_f} = 0.75\sqrt{G_{t_m t_m} G_{t_f t_f}}$, (e) $G_{t_m t_f} = \sqrt{G_{t_m t_m} G_{t_f t_f}}$. We assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $G_{t_m t_f} = 0.001$, $c_{RI} = 0.05$, $c = 0.1$, $a = 5$, $b = 5$, $d_m = d_f = 0.05$, $\lambda = 0$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.0025$, $t_a = 0$, $\bar{t}' = 1$.

At final state we have $\beta_{t_m}(\bar{t}_m^*) = 0$ (β_{t_m} is given in Equation (3). Because we have

$$\beta_{t_m}(t_a) = \frac{-2b(t_a - t')d_m \lambda' N' \exp\left[-b(t_a - t')^2\right]}{(1 + \lambda' N' \exp\left[-b(t_a - t')^2\right])^2} > 0,$$

and

$$\beta_{t_m}(t') = -2s(t' - t_a) < 0,$$

$\bar{t}_m^*$ is bounded by t_a and t'. Similar arguments give that final females trait is bounded by t_a and t'. Because $\bar{t}_m^*$ is the final trait we have $\forall \tau \in [t_a, \bar{t}_m^*[, \beta_{t_m}(\tau) > 0$.

For all trait τ we have

$$\beta_{t_f}(\tau) = \beta_{t_m}(\tau) - (d_f - d_m)\frac{2(\tau - t')\lambda' N' \exp\left[-b(\tau - t')^2\right]}{(1 + \lambda' N' \exp\left[-b(\tau - t')^2\right])^2},$$

which implies that $\forall \tau \in [t_a, t'[, \beta_{t_f}(\tau) > \beta_{t_m}(\tau)$. Then $\forall \tau \in [t_a, \bar{t}_m^*], \beta_{t_f}(\tau) > 0$. Therefore $\bar{t}_f^* > \bar{t}_m^*$ and then we have (A7).

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7 Sexual dimorphism is higher for low density of the *focal* species when reproductive interference is strong enough to promote divergence away from the mimetic trait in males.
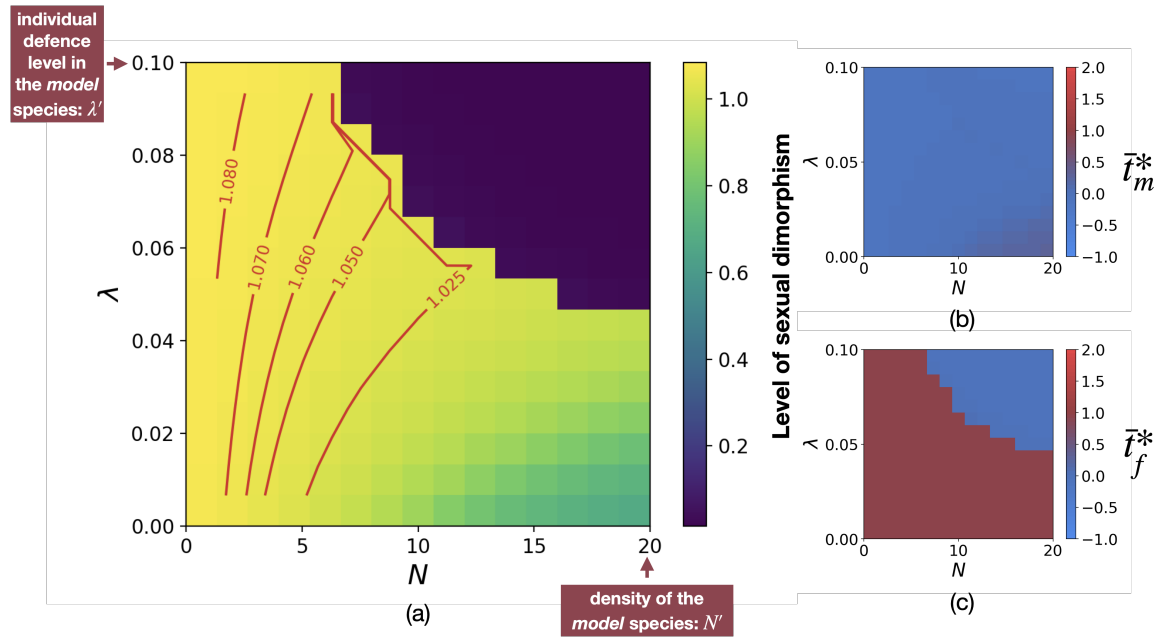

Figure A5: **Influence of the density N and of the individual defence level λ in the *focal* species on (a) the final level of sexual dimorphism $|\bar{t}_m^* - \bar{t}_f^*|$, (b) final males trait $\bar{t}_m^*$ and (c) final females trait $\bar{t}_f^*$ when female-limited mimicry is caused by RI via sexual selection (c_{RI} and $a > 0$) and not by sexually contrasted predation ($d_f > d_m$).** Along red lines the level of sexual dimorphism is constant. We assume: $G_{t_m} = G_{t_f} = G_{p_f} = 0.01$, $G_{t_m t_f} = 0.001$, $c_{RI} = 0.015$, $c = 0.1$, $a = 5$, $b = 5$, $d_m = d_f = 0.05$, $N = 10$, $\lambda' = 0.1$, $N' = 20$, $s = 0.0025$, $t_a = 0$, t'.