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

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Received July 22, 2021
Accepted July 18, 2022

The striking female-limited mimicry observed in some butterfly species is a text-book example of sexually dimorphic trait submitted to intense natural selection. Two main evolutionary hypotheses, based on natural and sexual selection respectively, have been proposed. Predation pressure favoring mimicry toward defended species could be higher in females because of their slower flight, and thus overcome developmental constraints favoring 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 female preference for non-mimetic males. However, the evolutionary origin of female preference for non-mimetic traits remains unclear. Here, we hypothesize that costly sexual interactions between individuals from 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 mimicry when assuming either alternative selective hypotheses. We show that the patterns of divergence of male and female trait from the ancestral traits can differ between these selection regimes. We specifically highlight that divergence in female trait is not a signature of the effect of natural selection. Our results also evidence why female-limited mimicry is more frequently observed in Batesian mimics.

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 evolution 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 emergence of elaborated traits in males only, therefore leading to sexual dimorphism (Darwin 1871). The relative contributions of natural and sexual selection to the evolution of sexually dimorphic traits has generated important controversies. The evolution of sexual dimorphism in wing color patterns in butterflies has been central to this debate because wing color patterns are under strong 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 one 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 wing colour pattern dimorphism is mainly driven by the divergence of male phenotype from the ancestral trait, in line with the sexual selection hypothesis. In contrast to this general trend, sexual dimorphism where females exhibit a derived color 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 reduced predation risk (Bates 1962, Ruxton et al. 2019). Despite predation...
affecting individuals from both sexes, mimicry is sometimes surprisingly limited to females (Ford 1975, Nishikawa et al. 2015, Kunte 2008, Long et al. 2014), therefore begging the question of the evolutionary forces preventing the evolution of mimicry in males (i.e. female-limited mimicry, named FLM hereafter).

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 & Wickman 1990) and muscle mass (Marden & Chai 1991), resulting in increased flight power (Chai & Srygley 1990). Predation pressures are thus expected to be stronger in females. In line with this expectation, Su et al. (2015) showed that in a mimetic butterflies where males and females mimic the same species, females are more perfect mimics than males, suggesting also that some constraints limits perfect mimicry in males. Wing pattern evolution is also shaped by developmental constraints (Van Belleghem et al. 2020) that may impede divergence from the ancestral trait (Maisonneuve et al. 2021). Phylogenetic analyses show that FLM derived from sexually monomorphic non-mimetic ancestors (Kunte 2009, Timmermans et al. 2017) suggesting that mimicry in FLM species is associated with a costly displacement from an ancestral non-mimetic phenotype. In the female-limited polymorphic butterfly *Papilio polytes*, where both mitec and non-mimetic females co-exist, the mimetic allele reduces the pre-adult survival rate (Komata et al. 2020, Katoh et al. 2020) (but see Komata et al. 2018 in the FLM butterfly *Papilio memnon*), highlighting cost associated with mimicry. Such trade-off between developmental constraints favoring 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. In line with this idea, in mimetic Asian pitvipers, where males suffer for a greater predation pressure, females are rarely mimic, strengthening the role of sexually contrasted predation in promoting sex-limited mimicry (Sanders et al. 2006). Nevertheless, evidence for the limited predation in males as compared to females is controversial in butterflies (Wourms & Wasserman 1985) therefore questioning whether contrasted predation in males and females is actually the main driver of FLM.

Other constraints triggered by sexual selection might limit mimicry in males. In the female-limited Batesian mimic *Papilio polxenes asterius*, experimental alteration of male color pattern into female color pattern leads to lower success during male–male encounters and increased difficulty in establishing a territory, therefore reducing mating opportunities (Lederhouse & Scribe 1996). Furthermore, in the female-limited Batesian mimic *Papilio glaucus*, females prefer control painted non-mimetic males over painted mimetic males (Krebs & West 1988) (but see Low and Monteiro 2018 in the FLM butterfly *Papilio polytes*). Wing color patterns in mimetic butterflies may therefore modulate male reproductive success, by influencing both male-male competition and mating success with females. In particular, female 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 are predicted to prefer mimetic males because it leads to adapted mimetic offspring, favouring 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, Kronforst et al. 2006, Merrill et al. 2014, Naisbit et al. 2001). It is thus unclear what does limit the evolution of female preference toward mimetic coloration in males from mimetic species.

Female preference for mimetic males may be disadvantageous because this behavior may lead to mating interactions with unpalatable “model” species. Therefore reproductive interference, that is, costly interactions between different species during mate acquisition (see Gröning and Hochkirch 2008 for a definition), may impair the evolution of female preference towards mimetic color patterns displayed by other sympatric species. The evolution of mimetic coloration in males may indeed increase costs linked to reproductive interference in females, and therefore promote the evolution of preference for non-mimetic traits in males. Such reproductive interference has been observed between species sharing similar aposematic traits (in *Heliconius* and *Mechanitis* species, Estrada & Jiggins 2008). The rate of erroneous mating may be limited by the difference in male phenomemes 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 reproductive interference, even if they refuse mating with heterospecific males: females may allow courting by heterogeneous 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 color pattern then need to deploy substantial efforts to avoid the heterospecific mating.

Theoretical studies highlight that the reproductive interference between sympatric species influence the evolution of traits used as mating cues. Reproductive interference indeed promotes the evolution of female preference toward traits differing from the phenotype displayed in other sympatic species, because it
reduces the number of costly sexual interactions (McPeek & Gavrilets 2006, Maisonneuve et al. 2021, Yamaguchi & Iwasa 2013). However these studies do not consider the independent evolution male and female traits. Under weak constraint on sex differentiation, reproductive interference may impede divergence of male trait, while natural selection may promote the evolution of female trait, leading to sexual dimorphism. For instance, in two of the three fruit fly species of the genus Blepharoneura that court on the same host plant, a morphometric analysis reveals sexual dimorphism in wing shape where males, but not females, from the two different species differ in wing shape (Marстeller et al. 2009). In the mexican spadefoot toads Spea multiplicata, the level of sexual size dimorphism increases with the proportion of species from the same genus Spea bombifrons living in sympatry (Pfennig & Pfennig 2005) suggesting a link between species interactions and sexual dimorphism. In species exhibiting FLM, reproductive interference may thus inhibit natural selection in males, when females become mimetic. Theoretical studies show that reproductive interference can totally impair the evolution of mimicry (Boussens-Dumon & Llaurens 2021) or lead to imperfect mimicry (Maisonneuve et al. 2021) therefore suggesting that reproductive interference might indeed be a relevant ecological interaction preventing mimicry in males. In the model investigating the effect of reproductive interference on mimicry described in Boussens-Dumon and Llaurens (2021), color-pattern based assortative mating was assumed, preventing the study of the evolution of disassortative preferences in females. Therefore understanding the impact of reproductive interference on the evolution of FLM, requires to specifically explore the evolution of female preference, and to assume a genetic architecture enabling mating cues to evolve in different directions in males and females.

Interestingly, the two main hypotheses usually explaining FLM, that is, (1) sexually contrasted predation and (2) sexual selection on males, are both equally relevant for palatable, as well as unpalatable mimetic 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 & 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) reproductive interference and (2) sexually contrasted predation may promote the evolution of FLM, using a mathematical model. First, we pinpoint the specific evolutionary outcomes associated with the emergence of FLM driven by reproductive interference or sexually contrasted predation, therefore providing relevant predictions for comparisons with empirical data. Second, 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 exhibiting a fixed warning trait. 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 reproductive interference paid by females from the “focal” species (McPeek & Gavrilets 2006, Yamaguchi & Iwasa 2013). We assume that a mating 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 & 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 reproductive interference 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 sympathy with a defended species displaying a fixed warning trait (referred to as the model species hereafter). Within the model species, all individuals display the same warning trait. We investigate the evolution of the warning trait expressed in the focal species, influenced by both (1) predators behavior promoting mimicry toward 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 favoring 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 close to the mean trait $\bar{t}$, 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 behavior of predators. This resemblance towards the model species then induces costs for individuals from the focal species, caused by reproductive interference. These reproductive interference 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 & 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. Natural selection acting on an individual depends on the trait \( t \) expressed. We note \( W_{ns}^\sigma(t_m) \) and \( W_{ns}^\varphi(t_f) \) (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 \( W_i(t_m, p_f) \) (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) reproductive interference 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:

\[
W(t_m, t_f, p_f) = W_{ns}^\sigma(t_m)W_i(t_m, p_f)W_{ns}^\varphi(t_f). \tag{1}
\]

We assume that the variance of traits and preference is small relative to the curvature of the fitness function, which is a weak selection assumption (Iwasa et al. 1991, Pomiankowski & Iwasa 1993). Using the Price’s theorem (Rice 2004), we can approximate the change in the mean values of traits \( \hat{t}_m, \hat{t}_f \), and preference \( \hat{p}_f \) in the focal species after the natural and sexual selection respectively by:

\[
\begin{pmatrix}
\Delta \hat{t}_m \\
\Delta \hat{t}_f \\
\Delta \hat{p}_f
\end{pmatrix}
= \frac{1}{2}
\begin{pmatrix}
G_{t_m t_m} & G_{t_m p_f} & G_{t_f p_f} \\
G_{t_m p_f} & G_{p_f p_f} & G_{p_f p_f} \\
G_{t_f p_f} & G_{p_f p_f} & G_{p_f p_f}
\end{pmatrix}
\begin{pmatrix}
\hat{\beta}_m \\
\hat{\beta}_f \\
\hat{\beta}_p
\end{pmatrix}, \tag{2}
\]

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

\[
\begin{pmatrix}
\hat{\beta}_m \\
\hat{\beta}_f \\
\hat{\beta}_p
\end{pmatrix}
= \begin{pmatrix}
\frac{d}{dt_m} \log W(t_m, t_f, p_f) \\
\frac{d}{dt_f} \log W(t_m, t_f, p_f) \\
\frac{d}{dp_f} \log W(t_m, t_f, p_f)
\end{pmatrix}_{(t_m, t_f, p_f) = (\hat{t}_m, \hat{t}_f, \hat{p}_f)}, \tag{3}
\]

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

Under the weak selection assumption, genetic correlations generated by selection and non-random mating quickly reach equilibrium (Nagylaki 1993) and can thus be approximated by their equilibrium values.

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 \( G_{t_at_f} \) 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 \( G_{t_at_f} = 0 \) would describe a situation where the genetic architecture coding for traits expressed in males and females. For example \( G_{t_at_f} = 0 \) 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 nonrandom mating generates genetic association between \( t_m \) and \( p_f \). Under weak selection assumption \( G_{t_m p_f} \) is assumed to be at equilibrium. This quantity is given by (see Appendix 2):

\[
G_{t_m p_f} = aG_{t_m t_m}G_{p_f p_f}, \tag{4}
\]

where \( a \) quantifies how frequently 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 (4 a) in Lande & Arnold (1985), we have

\[
G_{t_f p_f} = G_{t_m t_m}G_{p_f p_f}. \tag{5}
\]

**ANCESTRAL TRAIT VALUE \( t_a \)**

To investigate the effect of reproductive interference on the evolution of sexual dimorphism, we study the evolution of male and female traits \( (t_m, t_f) \) 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 \( W_{pred}^\sigma \) and \( W_{pred}^\varphi \) for males and females respectively. It is thus given by:

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

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

We assume \( s \) to be of order \( \epsilon \), with \( \epsilon \) small, therefore enabling to apply the weak selection assumption.

**PREDATION PRESSURE EXERTED ON WARNING TRAIT**

Predators exert 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, Chouteau et al. 2016, Mallet & Barton 1989), due to predators learning. The density-dependence is modulated by the individual defence level \( \lambda \), shaping predator deterrence: the higher the defence, the higher the defended individual contributes to the learning of predators. We note \( \lambda ' \) 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:

\[
\mathcal{D}(t) = \int_{a}^{b} \lambda N \frac{f^{\otimes}(t_m)}{2} \exp\left(-b(t - t_m)^2\right) dt_m + \int_{c}^{d} \lambda N' g(t') \exp\left(-b(t - t')^2\right) dt'.
\]

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

Because we assume that traits variance is small relative to the curvature of the fitness function within both the focal and the model species we can approximate (8) by (see Appendix 3):

\[
\mathcal{D}(t) \approx \lambda N \frac{N}{2} \exp\left(-b(t - t_m)^2\right) + \lambda N' \frac{N'}{2} \exp\left(-b(t - t')^2\right).
\]

When a female with preference \( p_f \) encounters a male displaying the trait value \( t_m \), the mating occurs with probability:

\[
\exp\left[-a(p_f - t_m)^2\right],
\]

when the encountered male is a conspecific or

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

when the encountered male belongs to the model species. Female choosiness \( a \), assumed constant among females, quantifies how frequently 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):

\[
T(p_f) = \int_{a}^{b} \frac{N}{N + N'} f^{\otimes}(t_m) \exp\left[-a(p_f - t_m)^2\right] dt_m.
\]

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

\[
T_{RI}(p_f) = \int_{c}^{d} \frac{N'}{N + N'} g(t') c_{RI} \exp\left[-a(p_f - t')^2\right] dt'.
\]
Figure 1. Computation of the contribution to the next generation of a mating. During an encounter, a female expresses her preference toward 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.

Because the variance of traits within both the focal and the model species is small relative to the curvature of fitness function we have the following approximations:

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

and

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

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:

$$\phi(p_f, t_m) = \frac{\exp \left[ -a(p_f - t_m)^2 \right] f_{\sigma}(t_m)}{\int_{\tau_m} \exp \left[ -a(p_f - \tau)^2 \right] f_{\sigma}(\tau) d\tau}. \quad (17)$$

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

$$\phi(p_f, t_m) \approx \frac{\exp \left[ -a(p_f - t_m)^2 \right] f_{\sigma}(t_m)}{\exp \left[ -a(p_f - \bar{t}_m)^2 \right]} \quad (18)$$

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

$$P_1(p_f, t_m) = h(p_f) T(p_f) \frac{\exp \left[ -a(p_f - t_m)^2 \right] f_{\sigma}(t_m)}{\exp \left[ -a(p_f - \bar{t}_m)^2 \right]}, \quad (19)$$

where $h$ is the distribution of preferences in the population.
Table 1. Description of variables and parameters used in the model.

| 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 |
| $a$ | Female choosiness in the focal species |
| $s$ | Strength of developmental constraints in the focal species |
| $t_0$ | Ancestral trait favoured by developmental constraints in the focal species |
| $t'$ | Trait displayed in the model species |
| $d_m/d_f$ | Basic predation rate in males and females respectively |
| $b$ | Predator discrimination |
| $\lambda_0/\lambda_1$ | 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 |

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

$$P(p_f, t_m) = \sum_{i=0}^{\infty} \frac{\left((1 - T(p_f) - T_{R0}(p_f))(1 - c)\right)^i P^1(p_f, t_m)}{c + (1 - c)(T(p_f) + T_{R0}(p_f))},$$

(20)

where $\left((1 - T(p_f) - T_{R0}(p_f))(1 - c)\right)^i$ 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 preference $p_f$, $W_i(t_m, p_f)$, is thus given by (see Figure 1)

$$W_i(t_m, p_f) = \frac{T(p_f)}{c + (1 - c)(T(p_f) + T_{R0}(p_f))} \times \frac{\exp \left[-a(p_f - t_m)^3\right]}{\exp \left[-a(p_f - \bar{T}_m)^3\right]}$$

(21)

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

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 $t_0$.

We 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). In Appendix 4, we explore two alternative scenarios: where the focal and the model species (1) ancestrally share common predators promoting mimicry before entering sexually in contact or (2) ancestrally interact sexually before sharing a common predator promoting mimicry.

Numerical simulations of the quantitative model

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

$$\left\| \begin{bmatrix} \Delta T_m \\ \Delta T_f \\ \Delta p_f \end{bmatrix} \right\|_2 < 3 \times 10^{-11}.$$  (22)

Individual-centred simulations

We also run individual-centered simulations with explicit genetic architecture to study the evolution of FLM with strong selection, as well as with high and fluctuating genetic variance of traits and preference. We assume two genetic architectures in an haploid population:

- Independent genetic basis of male and female trait: we assume three loci $T_m$, $T_f$, and $P_f$, coding respectively for male trait, female trait and preference. We assume a large number of alleles at each locus, where each allele is associated with a real number, corresponding to the value of the trait or of the preference. We assume recombination rate between each loci $r_{T_m,T_f}$ and $r_{T_m,P_f}$.
- Partially common genetic basis of male and female trait: we assume four loci $T_1$, $T_2$, $T_3$, and $P_f$. Locus $T_2$ controls the trait variations shared by males and females and loci $T_1$ and $T_3$ (resp. $T_2$ and $T_3$) codes for specific male (resp. female) trait value
with additive effect. \( P_t \) codes for female preference value. We assume a large number of alleles at each locus, where each allele is associated with a real number. We assume recombination rate between each loci \( r_{TiTj}, r_{TfTj}, \) and \( r_{TiPf}. \)

We assume non-overlapping generations and constant population size. At each generation, we first model the effect of natural selection. The survival of an individual follows a Bernoulli distribution, where the probability of surviving is given by the fitness component due to natural selection (see Equations (6) and (6)).

Second, females and males meet uniformly at random. Female acceptance of a potential male follows a Bernoulli distribution, where the acceptance probability is given by Equation (11) (resp. (12)) if the potential male is a conspecific (resp. heterospecific). Females pay a fertility cost when attempting mating with an heterospecific male. Females may also pay a fertility cost when refusing a mating opportunity, depending on cost of choosiness \( c. \)

Third, a mutation appears at each allele in the new generation. Each mutation follows a normal distribution centered on the value associated with the allele. We model the mutation effect across all loci using a constant standard deviation \( \mu. \) We also assume an initial genetic variance of trait and preference \( G_0, \) and no genetic covariance. We run individual-centered simulations across 10,000 generations. Final trait and preference values are given by the mean value across the 1000 last generations. We run replicates for each parameter value and we provide the number of replicate runs in the caption of each figure.

**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 reproductive interference \( (c_{RI} \) and \( a > 0) \) and \( (2) \) sexually contrasted predation \( (d_f > d_m). \) We thus compute the equilibrium traits and preference \( (t_{em}^*, t_{fm}^*, \phi_f) \) for different strengths of reproductive interference \( (c_{RI} \in [0, 0.1]) \) or different basic 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 \( |t_{em}^* - t_{fm}^*|. \)

**Figure 2.** Illustration of the three main outcomes: (a) male trait value in the focal species gets closer to the value displayed in the model species \( t', \) (b) male 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 male 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.

**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

\[
\phi = |t_{em}^* - t_a| - |t_{fm}^* - t_a|.
\]

When \( \phi < 0 \) we have \( |t_{em}^* - t_a| > |t_{fm}^* - t_a| \) thus the trait diverged more in females than in males (see an illustration in Figure 2a and b). By contrast \( \phi > 0 \) indicates that the trait diverged more in males than in females (see an illustration in Figure 2c). We compare this sexual bias in phenotypic divergence under the two hypothetical mechanisms of FLM, to determine whether this criterion could be used to infer the actual evolutionary pressures involved in the emergence of FLM in natural populations.

We first study the values of sexual bias in phenotypic divergence when reproductive interference causes FLM \( (c_{RI} = 0.01), \) using numerical simulations. We investigate the effect of two key parameters: female choosiness \( a \) modulating cost of reproductive interference 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 Figure 2b and c). We then study the sexual bias in phenotypic divergence when FLM stems from sexually contrasted predation ($d_f > d_m$), by deriving analytical results standing for all parameters value (see Appendix 5).

**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 level ($\lambda \in [0, 0.1]$) on equilibrium traits ($t^*_m$, $t^*_f$) and the level of sexual dimorphism ($t^*_m - t^*_f$). Because males and females in the focal species can display different traits, the level of protection 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 by the individual level of defence in the focal species ($\lambda$). When males from the focal species are non-mimetic, their defence level is given by the individual level of defence $\lambda$ and the density of males $N/2$. To investigate the impact of defence level on the emergence of FLM, we thus explore not only the effect of the individual defence level $\lambda$, but also of the density of the focal species ($N \in [0, 20]$).

The effects of all explored parameters and evolutionary forces on the evolution of FLM are summed up in Figure 3.

**Results**

**REPRODUCTIVE INTERFERENCE PROMOTES FEMALE-LIMITED MIMICRY IN PALATABLE SPECIES**

We first test whether reproductive interference can generate FLM in a harmless species ($\lambda = 0$). We thus investigate the impact of the strength of reproductive interference ($c_{RI}$) on the evolution of male trait ($t^*_m$), female trait and preference ($t^*_f$ and $p^*_f$), for different levels of female choosiness ($a$) modulating the costs generated by the strength of reproductive interference (Figure 4a). Without reproductive interference ($c_{RI} = 0$), both males and females in the focal species are mimetic at equilibrium and the sexual dimorphism therefore does not emerge (Figure 4a). By contrast, when assuming reproductive interference ($c_{RI} > 0$), FLM evolves in the focal species (Figure 4a, see temporal dynamics in Figure A5a). Reproductive interference promotes a greater distance between final female preference $p^*_f$ and the trait of the model species $t'$. Such female preference for non-mimetic males reduces costly sexual interactions with heterospecific males of the model species and generates sexual selection on male trait, inhibiting mimicry in males. Reproductive interference also promotes FLM in alternative scenarios when the focal and the model species (1) ancestrally share common predators promoting mimicry before entering sexually in contact or (2) ancestrally interact sexually before sharing a common predator promoting mimicry (see Appendix 4). Because FLM strongly
Influence of (a) the strength of reproductive interference ($c_{RI}$) and (b) female choosiness ($a$) on the equilibrium values of male trait $\tilde{t}_m^*$ (yellow solid line), female trait $\tilde{t}_f^*$ (purple solid line) and female preference $\overline{p}_f^*$ (purple dashed line). By default we assume: $G_{mf} = G_{tf} = G_{pf} = 0.01$, $G_{mf,f} = 0.001$, $c_{RI} = 0.01$, $c = 0.1$, $a = 10$, $b = 5$, $d_m = d_f = 0.05$, $\lambda = 0$, $N = 100$, $\lambda' = 0.01$, $N' = 200$, $s = 0.0025$, $t_0 = 0$, $\overline{t} = 1$.

Figure 4. Influence of (a) the strength of reproductive interference $c_{RI}$ and (b) female choosiness $a$ on the equilibrium values of male trait $\tilde{t}_m^*$ (yellow solid line), female trait $\tilde{t}_f^*$ (purple solid line) and female preference $\overline{p}_f^*$ (purple dashed line). By default we assume: $G_{mf} = G_{tf} = G_{pf} = 0.01$, $G_{mf,f} = 0.001$, $c_{RI} = 0.01$, $c = 0.1$, $a = 10$, $b = 5$, $d_m = d_f = 0.05$, $\lambda = 0$, $N = 100$, $\lambda' = 0.01$, $N' = 200$, $s = 0.0025$, $t_0 = 0$, $\overline{t} = 1$.

depends on the evolution of female preference for potentially scarce non-mimetic males, it emerges only when the cost of choosiness ($c$) is low (see Appendix 7 for more details). FLM also evolves only when male and female traits have at least partially different genetic basis, allowing divergent evolution between sexes. The genetic covariance between male and female trait $G_{mf,f}$ then only impacts the time to reach the equilibrium (see Appendix 8 for more details).

We also investigate the impact of female choosiness ($a$) (modulating the stringency of sexual selection and cost of reproductive interference) on FLM, when there is reproductive interference ($c_{RI} > 0$) (Figure 4(b)). The relationship between the final male trait value and the parameter $a$ is sometimes discontinuous because for close value of parameters, the evolutionary dynamics can take different paths. When $a$ is close to 0, both males and females become mimetic to the model species (Figure 4b). In this case, non-choosy females tend to accept almost all males, despite their preference $p_f$. Thus selection on female preference $p_f$ is low because a change on preference hardly changes the mating behavior and the resulting cost of reproductive interference. When $a$ is higher than 0 and approximately lower than 5, selection due to reproductive interference on preference is important and reproductive interference 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 $t_0$ (Figure 4b, see Figure 2b for an illustration and Figure A5b for temporal dynamics). Such divergence from the ancestral trait in males does not occur when female choosiness is higher ($a \geq 5$ in Figure 4b, see Figure 2a for an illustration): when females are more picky, a small difference between female preference and the mimetic trait sufficiently reduces the cost of reproductive interference (Figure 4b). All results described in this section are confirmed in individual-centered simulations assuming simple genetic architecture of traits and preference (Figures A10 and A11), highlighting that the weak selection, constant and low genetic variance assumptions do not preclude obtaining relevant analytical predictions.

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 basic predation rate on males and females ($d_m/d_f$) on the evolution on FLM (Figure 5a) in case without reproductive interference 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 5a, and see temporal dynamics in Figure A5c). 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 5a). When males and females suffer from similar predation pressure (i.e., $d_m/d_f = 1$), both sexes become mimetic (Figure 5a).

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, because males become mimetic even if they suffer for low predation (Figure 5b). By
Influence of (a) the ratio of basic predation rate on males and females $d_m/d_f$ and (b) the strength of developmental constraints $s$ on the equilibrium values of male trait $t^*_m$ (yellow solid line), and female trait $t^*_f$ (purple solid line). By default we assume: $G_{tm} = G_{tf} = G_{p_f} = 0.01$, $G_{tmf} = 0.001$, $c_{df} = 0$, $c = 0$, $a = 0$, $b = 5$, $d_m = 0.005$, $d_f = 0.05$, $\lambda = 0$, $N = 100$, $\lambda = 0.01$, $N' = 200$, $s = 0.01$, $t_a = 0$, $t' = 1$. 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 6b). 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 overcome 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 6a).

The relationship between the final male trait and the parameters is discontinuous as previously highlighted, leading to three zones within where male trait vary continuously. When female choosiness is low (zone A, $a \lesssim 1.8$), the selection caused by reproductive interference is mild: females are not very choosy and thus tend to accept almost all males despite their preference $p_f$, therefore relaxing selection on female preference, and favoring 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 a so-called “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 male trait, even for low values of female choosiness ($a \lesssim 1.8$).

However, when female choosiness has intermediate values ($1.8 \lesssim a \lesssim 4$, zone B), enhanced female choosiness increases selection due to reproductive interference 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. Using individual-centered simulations, we then show that stochastic variations may result in the contrast, in individual-centered simulations, male trait becomes highly variable due to a lack of selection, whereas female trait under strong predation pressure, has a low variance (Figure A13). Relaxed selection on males may allow trait values leading to poor mimicry to emerge in males, while the stronger selection on females favors their accurate mimicry. This sexually different selection regime thus increases sexual dimorphism. 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) (Figure 5b). Important developmental constraints ($s \gtrsim 0.7$) overcome the advantages provided by mimicry in both sexes, and prevent the evolution of sexual dimorphism (Figure 5b). Beside the case previously mentioned, all results shown in this section still hold in our individual-centred simulations (Figures A12 and A13).

DIFFERENT HYPOTHETICAL CAUSES OF FEMALE-LIMITED MIMICRY LEAD TO DIFFERENT PREDICTIONS

Here, we use our mathematical model to compare the effect of (1) reproductive interference 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 reproductive interference via sexual selection ($a > 0$ and $d_f = d_{df}$). 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 $|t^*_m - t_a| - |t^*_f - t_a|$. Figure 6 highlights that divergence from the ancestral trait can be stronger in males (yellow zone on Figure 6c) or in females (purple zone on Figure 6c) depending on these parameters.

In Figure 5. Influence of (a) the ratio of basic predation rate on males and females $d_m/d_f$ and (b) the strength of developmental constraints $s$ on the equilibrium values of male trait $t^*_m$ (yellow solid line), and female trait $t^*_f$ (purple solid line). By default we assume: $G_{tm} = G_{tf} = G_{p_f} = 0.01$, $G_{tmf} = 0.001$, $c_{df} = 0$, $c = 0$, $a = 0$, $b = 5$, $d_m = 0.005$, $d_f = 0.05$, $\lambda = 0$, $N = 100$, $\lambda = 0.01$, $N' = 200$, $s = 0.01$, $t_a = 0$, $t' = 1$. 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 6b). 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 overcome 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 6a).

The relationship between the final male trait and the parameters is discontinuous as previously highlighted, leading to three zones within where male trait vary continuously. When female choosiness is low (zone A, $a \lesssim 1.8$), the selection caused by reproductive interference is mild: females are not very choosy and thus tend to accept almost all males despite their preference $p_f$, therefore relaxing selection on female preference, and favoring 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 a so-called “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 male trait, even for low values of female choosiness ($a \lesssim 1.8$).

However, when female choosiness has intermediate values ($1.8 \lesssim a \lesssim 4$, zone B), enhanced female choosiness increases selection due to reproductive interference 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. Using individual-centered simulations, we then show that stochastic variations may result in the contrast, in individual-centered simulations, male trait becomes highly variable due to a lack of selection, whereas female trait under strong predation pressure, has a low variance (Figure A13). Relaxed selection on males may allow trait values leading to poor mimicry to emerge in males, while the stronger selection on females favors their accurate mimicry. This sexually different selection regime thus increases sexual dimorphism. 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) (Figure 5b). Important developmental constraints ($s \gtrsim 0.7$) overcome the advantages provided by mimicry in both sexes, and prevent the evolution of sexual dimorphism (Figure 5b). Beside the case previously mentioned, all results shown in this section still hold in our individual-centred simulations (Figures A12 and A13).

DIFFERENT HYPOTHETICAL CAUSES OF FEMALE-LIMITED MIMICRY LEAD TO DIFFERENT PREDICTIONS

Here, we use our mathematical model to compare the effect of (1) reproductive interference 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 reproductive interference via sexual selection ($a > 0$ and $d_f = d_{df}$). 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 $|t^*_m - t_a| - |t^*_f - t_a|$. Figure 6 highlights that divergence from the ancestral trait can be stronger in males (yellow zone on Figure 6c) or in females (purple zone on Figure 6c) depending on these parameters.
EVOLUTIONARY ORIGINS OF SEXUAL DIMORPHISM

Figure 6. Influence of the distance between the ancestral and the mimetic traits \( |t' - t_a| \) and of female choosiness \( a \) on (a) final male trait \( \bar{t}_m^* \), (b) final female trait \( \bar{t}_f^* \), and (c) the difference between the level of divergence in males and females \( |\bar{t}_m^* - t_a| - |\bar{t}_f^* - t_a| \). Note that Figure 6c results from Figure 6a and b. Yellow lines indicate equal levels of trait value. We assume: \( G_{tm} = G_{tf} = G_{pf} = 0.01 \), \( c_{RI} = 0.01 \), \( c = 0.1 \), \( b = 5 \), \( d_m = d_f = 0.05 \), \( \lambda = 0 \), \( N = 100 \), \( \lambda' = 0.01 \), \( N' = 200 \), \( s = 0.0025 \), and \( t' = 1 \).

The evolution of FLM caused by reproductive interference therefore leads to different divergence patterns, including divergence of male phenotypes away from the ancestral trait value, when the initial distance between the ancestral trait and the mimetic trait is low \((|t_a - t'| \simeq 0)\) (see Figure A19).

Contrastingly, high levels of choosiness in females \((a \geq 4\), zone C\) promote the evolution of more mimetic males because even a slight difference between the female preference and the mimetic trait allows to reduce cost of reproductive interference. 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 reproductive interference, despite the high pickiness \((i.e., high a)\) of females.

The evolution of FLM caused by reproductive interference 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 5 and see Figure 2a for an illustration). Individual-centered simulations confirm this pattern, except when the distance between the ancestral trait and the mimetic trait is low \((|t_a - t'| \simeq 0)\) (Figure A17). In this case, developmental constraints and predation promote the same trait value \((t_a \simeq t')\). The higher stabilizing selection in females, caused by a higher predation pressure, implies that female trait diverge less from the ancestral trait than males (Figure A19).

While both the reproductive interference and the sexually contrasted predation may result in FLM, the evolutionary pathways causing the sexual dimorphism are strikingly different. These results are generally maintained when relaxing the weak selection, constant and low genetic variance assumptions (see Appendix 11).

THE EVOLUTION OF FLM DEPENDS ON DEFENCE LEVEL

We then investigate the impact of the individual defence level \((\lambda)\) 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 reproductive interference via sexual selection (Figure 8).

Surprisingly, when FLM is caused by sexually-contrasted predation \((d_f > d_m)\), the level of sexual dimorphism can either increase or decrease with defence levels in both males and females \((\lambda N/2)\), depending on the strength of developmental constraints (Figure 7). In both sexes, the increase in defence levels
influence of the density \( N \) and of the individual defence level \( \lambda \) in the focal species on the equilibrium values of the level of sexual dimorphism \( |t^* - t^*_f| \) for different strength of developmental constraints \( (a) s = 0.01 \) \( (b) s = 0.02 \) 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: \( G_{t_m} = G_{t_f} = G_{P_f} = 0.01, G_{t_{mf}} = 0.001, c_{RI} = 0, c = 0, b = 5, d_m = 0.01, d_f = 0.05, \lambda' = 0.01, N' = 200, t_s = 0, t' = 1. \)

Indeed reduces selection favoring mimicry, while the developmental and selective constraints favor ancestral trait value. Great strength of developmental constraints \( (s = 0.02) \) then totally limits mimicry in males for every defence levels (Figure A21a). An increase in defence levels reduces mimicry in females (Figure 21b) but not in males that always displays the ancestral trait resulting in a decrease of the level of sexual dimorphism (Figure 7b). By contrast, low strength of developmental constraints \( (s = 0.01) \) allow the evolution of imperfect mimicry in males. However, the evolution of such mimicry in males is strongly impaired when defence level increases. In this range of mild levels of defence, mimicry is nevertheless advantageous in heavily attacked females (Figure A20b), resulting in high level of sexual dimorphism (Figure 7a). However, when the defence level becomes very high, both males and females display the ancestral trait, and sexual dimorphism is no longer observed (Figures A20 and A21 at the top right). Because of the high level of defence, individuals of both sexes gain sufficient protection from similarity with their conspecifics, relaxing selection promoting mimicry towards the model species. Individual-centered simulations provide the same patterns. Interestingly, the only discrepancy is observed for the effect of the density of the focal species when developmental constraints are low: in this case, the level sexual dimorphism no longer increases with with density of the focal species(see Appendix 13), contrary to what was observed in the deterministic model (A21a)). Stochasticity of population mean male and female trait values that is likely to increase sexual dimorphism. The amplitude of this stochastic effect reduce with population density that decrease the level of sexual dimorphism because when traits evolves randomly it is likely to produce sexual dimorphism (see figure A27).

Similarly, when FLM is caused by reproductive interference \( (c_{RI} > 0) \) via sexual selection, the level of sexual dimorphism can also either increase or decrease with the individual defence level \( \lambda \) depending on the strength of developmental constraints (Figures 8a and A22a). In contrast with predation differences between sexes, sexual selection induced by reproductive interference generates markedly higher sexual dimorphism for low values of density of the focal species \( (N < N' + 4) \) (Figure 8a). The relative density of the focal and the model species indeed determines the probability that a female of the focal species encounters a conspecific rather than a heterospecific male and thus modulate the costs of reproductive interference. Therefore, when the density of the focal species \( N \) is low, costs of reproductive interference are great, generating higher selection promoting sexual dimorphism. The density of the focal species therefore impacts much more the level of sexual dimorphism than the individual defence level \( \lambda \).

Under both hypotheses explaining female limited-mimicry, when developmental constraints totally inhibit mimicry in males, sexual dimorphism decrease with the level of defence. Under the assumption of sexual selection generated by reproductive interference however, sexual dimorphism is higher when the focal species is rarer than the model species. Under both selective hypotheses, mimicry toward the sympatric defended model species is no longer promoted in either sexes, when the level of defence within the focal species is high (Figures A20, A21, and 8b and c).
Figure 8. Influence of the density $N$ and of the individual defence level $\lambda$ in the focal species on the equilibrium values of (a) the level of sexual dimorphism $|t^*_m - t^*_f|$, (b) male trait $t^*_m$, and (c) female trait $t^*_f$ when female-limited mimicry is generated by sexual selection caused by reproductive interference ($c_{RI}$, $a > 0$ and $d_f = d_m$). Red and yellow lines indicate equal levels of sexual dimorphism and trait value, respectively. We assume: $G_{tm} = G_{tr} = G_{pf} = 0.01$, $G_{int} = 0.001$, $c_{RI} = 0.01$, $c = 0.1$, $a = 5$, $b = 5$, $d_m = d_f = 0.05$, $\lambda' = 0.01$, $N' = 200$, $s = 0.02$, $t_a = 0$, $t' = 1$.

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) female preference generated by reproductive interference can favor the evolution of FLM. By explicitly studying how these contrasted selective pressures influence the divergence of male and female trait from a common ancestral trait, our model sheds light on contrasted evolutionary pathways toward sexual dimorphism. Empirical studies based on the estimation of the level of divergence in male and female trait usually interpret elevated divergence in male 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 female trait, and concluded that FLM is caused by natural selection. However, our results show that when reproductive interference induces female 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.

Contrary to reproductive interference, sexually contrasted predation can generate FLM only when the focal and the model species have different ancestral traits. Such mechanism would thus be especially relevant for distantly related co-mimetic species, that are more likely to have divergent ancestors. In contrast, the role of reproductive interference in generating FLM is probably more important in cases where mimetic and model species are more closely related. Our results also show that a non-mimetic ancestral state favor the emergence of FLM under sexually contrasted selection. Therefore, the FLM observed in *Papilio garamas*, which likely derived from a sexually monomorphic and mimetic ancestor (Kunte 2009), might be a good candidate to investigate the potential origin of FLM due to reproductive interference. Our results thus stress the need to infer the for ancestral levels of mimicry, as well as the phylogenetic distances between mimetic species and their co-mimics or model species to empirically investigate the effect of reproductive interference on the evolution of FLM.
THE LEVEL OF INVESTMENT OF MALES IN REPRODUCTION AND THE EVOLUTION OF FLM CAUSED BY REPRODUCTIVE INTERFERENCE

Our results show that reproductive interference can generate female 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 reproductive interference 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 (Balshine et al. 2002, Trivers 1972). However, this asymmetrical investment in offspring between males and females can vary in different Lepidoptera species. In some species, butterfly males provide a nuptial gift containing nutrients during mating (Boggs & 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 (Lamunyon 1997, Wiklund et al. 1993). 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 reproductive interference 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.

Even when females are the choosy sex, they can still have preference based on multiple cues reducing cost of reproductive interference. Butterflies express preference for pheromones that may strongly differ between closely related species (Darragh et al. 2017, González-Rojas et al. 2020) thus limiting cost of reproductive interference. Moreover, different micro-habitat preference may reduces interspecific interactions and then female probability of accepting a heterospecific male (Estrada & Jiggins 2002). In our model, the probability to reject an heterospecific male based on other trait than the warning trait is captured by the parameters $c_{RI}$. Our results show that reproductive interference can promote FLM even when $c_{RI}$ is low. As soon as $c_{RI}$ is non-null, reproductive interference lead to selection on female preference and the evolution of FLM depends on the relative importance of each evolutionary forces.

Because few studies investigate the sexual selection origin of FLM, empirical studies estimating the reproductive costs and benefits in both sexes are strongly lacking. Here, we explicit a mechanism by which sexual selection can generate FLM. We thus hope our theoretical work will encourage experimental approaches investigating the link between reproductive costs and FLM. Such studies may shed light on the actual role of sexual selection generated by RI on the evolution of FLM.

RELATIVE SPECIES ABUNDANCES AND DEFENCES AND THE EVOLUTION OF FEMALE-LIMITED MIMICRY

Our results show that, for both causes of FLM (reproductive interference or sexually contrasted predation), the level of sexual dimorphism decreases with the individual level of defence when developmental constraints totally inhibit mimicry in males. This prediction is consistent with the empirical observation reporting FLM mostly in Batesian mimics, although 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: 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., 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 the evolution of FLM.

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 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 of the defended models (Long et al. 2015, Prusa & Hill 2021). Undefended mimics can have a negative effect predator’s learning (Lindström et al. 1997, Rowland et al. 2010), suggesting that 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 mimics also increases the protection of imperfect mimics allowing the evolution of gradual Batesian mimicry (Kikuchi & Pfennig 2010). The relative density between the focal and the model species is especially important when assuming reproductive interference, because the costs generated by heterospecific interactions depend on the proportion of heterospecific males encountered by females. Our results show that reproductive interference 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 reproductive interference, the lower relative density of undefended species may promote FLM.
and therefore explain why FLM could be especially favored in Batesian mimics is reserved to undefended species.

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, therefore increasing the cost of reproductive interference for undefended females. Batesian mimics often emerge after their models, when the models warning trait is well known by predators (Prusa & Hill 2021), and this might reinforce the evolution of FLM caused by reproductive interference in Batesian mimics. Overall, our theoretical study stresses the need of ecology studies quantifying relative densities of mimetic defended and palatable species through time. Such field studies, as well as chemical ecology studies quantifying defence variations, are now crucial needed to understand the evolution of FLM, in Batesian and Müllerian mimics.

**SEXUAL CONFLICT LIMITING MALES ADAPTATION**

Our study highlight that different fitness optima among sexes, due to natural and sexual selection, drives the evolution of sexual dimorphism in both hypothesis explaining FLM. Different fitness optima may stem from sexually dimorphic morphology, leading to different flight ability and to sexually contrasted predation risk. But different sexual roles, such as different levels of physiological investments in offspring, may also leads to contrasted effect of trait variations on female and male fitness, generating so-called sexual conflicts (Parker 2006). Sexual conflicts classically involves the evolution of traits enhancing male mating success with multiple females, and of traits enhancing the rejection of non-preferred males in females (e.g., conflicting coevolution of genitalia in males and females (Brennan et al. 2010). FLM driven by reproductive interference provide an original example of sexual conflict: while mimicry would enhance survival in males, female preferences generated by reproductive interference and by their greater reproductive investment, prevent the evolution of mimetic trait in males. This is thus a relevant case-study of sexual conflict driving the evolution of sexual dimorphism. Similarly, costly exaggerated trait in males may be regarded as a results of sexual conflicts: female prefer this expensive trait sign of mate quality (handicap principle (Zahavi 1975)) leading to maladaptive trait disfavored by natural selection (Johnstone 1995). In black scavenger flies Sepsis cynipsea and Sepsis neocynipsea species differentiation of exaggerated male forelegs is higher in sympatric population (Baur et al. 2020), suggesting than species interactions may indeed be a key evolutionary force involved in the evolution of exaggerated trait in males. Reproductive interference is indeed expected to promote male exaggerated trait improving species recognition in females. However, evidences of the role of reproductive interference in the evolution of sexual dimorphism are still scarce. Our theoretical work on FLM highlights that conflict between natural selection promoting the same trait in different species and reproductive interference may generate sexual dimorphism. We thus hope our results will stimulate new research on the effect of ecological interactions between closely-related species on the evolution of sexual dimorphism.

**Conclusion**

Our model show that both sexually contrasted predation and reproductive interference (by promoting preference for non-mimetic males) may generate FLM. Our results therefore show that the patterns of divergence of male and female trait from ancestral state should be interpreted in light from the selection regime involved. Our model also reveals the important role of ecological interactions between sympatric species on the evolution of sexual dimorphism, highlighting the need to consider the role of reproductive interference in the phenotypic diversification in sympathy.

**AUTHOR CONTRIBUTIONS**

LM, VL, and CS conceived and designed the study. LM analyzed the model. LM wrote the manuscript with contributions from all authors. VL and CS supervised the thesis of LM.

**ACKNOWLEDGMENTS**

The authors would like to thank the ANR SUPERSGNE (ANR-18-CE02-0019) for funding the PhD of LM. This work was partially supported by the Chair “Modélisation Mathématique et Biodiversité” of VEOLIA- Ecole Polytechnique-MNHN-F.X.

**DATA ARCHIVING**

Codes are available online: github.com/Ludovic-Maisonneuve/evo-flm.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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

Figure A1: Effect of the history of species interactions on the dynamics of the mean male trait and female trait and preference values across generations given by the deterministic quantitative model.

Figure A2: Effect of the history of species interactions on the dynamics of the mean male trait and female trait and preference values across generations. Each plot shows the dynamics obtained from a single simulation of individual-centred model in a given scenario, assuming independent genetic basis of male and female trait.

Figure A3: Effect of the history of species interactions on the dynamics of the mean male trait and female trait and preference values across generations. Each plot shows the dynamics obtained from a single simulation of individual-centred model in a given scenario, assuming independent genetic basis of male and female trait.

Figure A4: Two independent replicate runs of the dynamics of the mean male trait and female trait and preference values across generations given by individual-centred simulations assuming independent genetic basis of male and female trait when mimicry evolves first (scenario 2).

Figure A5: Evolution of the mean male trait and female trait and preference values across generations (a)(b) when reproductive interference or (c) sexually contrasted predation promotes sexual dimorphism.

Figure A6: Influence of the strength of reproductive interference cRI and of the cost of choosiness c on the final level of sexual dimorphism |ts − tf | and final preference pR.

Figure A7: Influence of the strength of reproductive interference cRI and of the genetic covariance between male and female trait normalized by its maximum value.

Figure A8: Evolution of the mean male trait and female trait and preference values across generations for different genetic covariances between male and female trait Gtm tf when male trait gets closer to the mimetic trait.

Figure A9: Evolution of the mean male trait and female trait and preference values across generations for different genetic covariances between male and female traits Gtm tf when reproductive interference promotes divergence of male trait away from the mimetic trait.

Figure A10: Boxplots of final mean male (yellow) and female (purple) traits values for different strength of reproductive interference cRI using individual-centred simulations assuming (a) independent genetic basis or (b) partially common genetic basis of male and female trait.

Figure A11: Boxplots of final mean male (yellow) and female (purple) traits values for different female choosiness a using individual-centred simulations assuming (a) independent genetic basis or (b) partially common genetic basis of male and female trait.

Figure A12: Boxplots of final mean male (yellow) and female (purple) traits values for different ratio of basic predation rate on males and females dm/df using individual-centred simulations assuming (a) independent genetic basis or (b) partially common genetic basis of male and female trait.

Figure A13: Boxplots of final mean male (yellow) and female (purple) traits values for different strength of developmental constraints s using individual-centred simulations assuming either (a) independent genetic basis or (b) partially common genetic basis of male and female trait.

Figure A14: Influence of the distance between the ancestral and the mimetic traits |t′ − ta | and of female choosiness a on (a)(d) the difference between the level of divergence in males and females |ts − ta | − |ts − tf | (b)(e) final male trait ts and (c)(f ) final female trait tfm using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f ) partially common genetic basis of male and female trait.

Figure A15: Standard deviation associated with Figure A14 of (a)(d) the difference between the level of divergence in males and females |ts − ta | − |ts − tf |, (b)(e) final male m′f trait ts and (c)(f ) final female trait tfm using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f ) partially common genetic basis of male and female trait.

Figure A16: Boxplots of final mean male (yellow) and female (purple) traits values for different male defensiveness d using individual-centred simulations assuming either (a) independent genetic basis or (b) partially common genetic basis of male and female trait.

Figure A17: Influence of the distance between the ancestral and the mimetic traits |t′ − ta | and of predator discrimination b on (a)(d) the difference between the level of divergence in males and females |ts − ta | − |ts − tf |, (b)(e) final male trait ts and (c)(f ) final female trait tfm using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f ) partially common genetic basis of male and female trait.

Figure A18: Standard deviation associated with Figure A17 of (a)(d) the difference between the level of divergence in males and females |ts − ta | − |ts − tf |, (b)(e) final male m′f trait ts and (c)(f ) final female trait tfm using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f ) partially common genetic basis of male and female trait.

Figure A19: Boxplots of final mean male (yellow) and female (purple) traits values for different female choosiness a using individual-centred simulations assuming either (a) independent genetic basis or (b) partially common genetic basis of male and female trait.

Figure A20: Influence of the distance N and of the individual defence level d in the focal species on the equilibrium values of (a) male trait ts and (b) female trait tf when female-limited mimicry is caused by sexually contrasted predation (df > dm , a = 0).

Figure A21: Influence of the density N and of the individual defence level d in the focal species on the equilibrium values of (a) male trait ts and (b) female trait tf when female-limited mimicry is caused by sexually contrasted predation (df > dm , a = 0).

Figure A22: Influence of the density N and of the individual defence level d in the focal species on the equilibrium values of (a) the level of sexual dimorphism |ts − tf |, (b) male trait ts and (c) female trait tf when female-limited mimicry is generated by sexual selection caused by reproductive interference (cRI, a > 0 and df = dm).

Figure A23: Influence of the density N and of the individual defence level d in the focal species on the equilibrium values of the level of sexual dimorphism (|ts − tf |) for different distances between the ancestral and the mimetic traits ((a) |ta − t′| = 1 (b) |ta − t′| = 1.1) when female-limited mimicry is caused by sexually contrasted predation (df > dm , a = 0).
Figure A24: Influence of the density $N$ and of the individual defence level $\lambda$ in the focal species on the equilibrium values of (a)(d) the level of sexual dimorphism $|t^*-t^*|$, (b)(e) male trait $t^*$ and (c)(f) female trait $t^*$ when selective constraints are high using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f) partially common genetic basis of male and female trait.

Figure A25: Standard deviation associated with Figure A24 of (a)(d) the level of sexual dimorphism $|t^*-t^*|$, (b)(e) final male trait $t^*$ and (c)(f) final female trait $t^*$ when selective constraints are high, using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f) partially common genetic basis of male and female trait.

Figure A26: Influence of the density $N$ and of the individual defence level $\lambda$ in the focal species on the equilibrium values of (a)(d) the level of sexual dimorphism $|t^*-t^*|$, (b)(e) male trait $t^*$ and (c)(f) female trait $t^*$ when selective constraints are low using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f) partially common genetic basis of male and female trait.

Figure A27: Standard deviation associated with Figure A26 of (a)(d) the level of sexual dimorphism $|t^*-t^*|$, (b)(e) final male trait $t^*$ and (c)(f) final female trait $t^*$ when selective constraints are low, using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f) partially common genetic basis of male and female trait.

Figure A28: Influence of the density $N$ and of the individual defence level $\lambda$ in the focal species on the equilibrium values of (a)(d) the level of sexual dimorphism $|t^*-t^*|$, (b)(e) male trait $t^*$ and (c)(f) female trait $t^*$ when selective constraints are high using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f) partially common genetic basis of male and female trait.

Figure A29: Standard deviation associated with Figure A28 of (a)(d) the level of sexual dimorphism $|t^*-t^*|$, (b)(e) final male trait $t^*$ and (c)(f) final female trait $t^*$ when selective constraints are high, using individual-centred simulations assuming either (a)(b)(c) independent genetic basis or (d)(e)(f) partially common genetic basis of male and female trait.