Influence of mimicry on extinction risk in Aculeata: a theoretical approach

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ABSTRACT

Positive ecological interactions can play a role in community structure and species co-existence. A well-documented case of mutualistic interaction is Mullerian mimicry, the convergence of colour pattern in defended species living in sympatry. By reducing predation pressure, Mullerian mimicry may limit local extinction risks of defended species, but this positive effect can be weakened by undefended mimics (Batesian mimicry). While mimicry was well-studied in neotropical butterflies, it remains surprisingly poorly studied in wasps and bees (Hymenoptera: Aculeata). However, only females are defended in Aculeata and this female-limited defence may modulate the effect of Mullerian mimicry on extinction risks. Here, we focus on the effect of Mullerian mimicry on extinction risk in Aculeata, using a population dynamics model for two species. We show that Mullerian mimicry has a positive effect on species co-existence, but this effect depends on the sex-ratio. We found that the probability of extinction increases as the proportion of undefended males increases in the population, however co-existence still occurs if females are sufficiently abundant or noxious. Furthermore, we detected a destabilising effect of dual sex-limited mimicry (when each sex resembles a different model) on species co-existence. In a context of massive population decline caused by anthropic activities, our findings highlight the potential importance of Mullerian mimicry as an overlooked mechanism linked to extinction risk in wasp and bee species.

Keywords: Mullerian mimicry, mutualism, population dynamics, aculeata, sex-ratio, coexistence.

Introduction

45   The assemblage of species within habitat is strongly driven by historical factors and abiotic constraints. Yet,
46   community structure and co-existence of species are also likely to be shaped by ecological interactions, either
47   antagonistic (*e.g.,* competition, predation, parasitism) or facilitative interactions such as commensalism or
48   mutualism (Holt, 2013) influencing both species colonization and extinction risk. The impact of antagonistic
49   interactions on species co-existence and extinction have been extensively documented (Bruno et al., 2003), in
50   particular the role of competition (Chesson, 2000; Raup, 1994). However, the impact of facilitative interactions
51   on the composition of communities, and its underlying mechanisms, are much less studied. Such facilitation
52   can involve improvement of physical environment (Bertness & Callaway, 1994), plant-pollinator interaction
53   (Moeller, 2004) or associative defences against herbivores (Hay, 1986). Facilitative interaction between species
54   plays a major role for species co-existence in stressful environments (Kéfi et al., 2008), and may prevail over
55   the effect of competition (Gross, 2008). Positive ecological interactions have been shown to strongly affect
56   species co-existence (Bastolla et al., 2009; Bertness & Callaway, 1994; Bronstein, 1994). In turn, mutualistic
57   interactions may contribute to co-extinction dynamics, following the loss of a partner species. In the current
58   context of biodiversity loss, studying the impact of mutualistic interactions on species extinction risk is thus
59   especially relevant because co-extinction could be a major cause of species loss (Dunn et al., 2009; Koh et al.,
60   2004).

61   Mullerian mimicry, whereby multiple defended species living in sympatry display similar conspicuous
62   colour patterns, reducing individual predation risk (Müller, 1879), is a well-documented case of mutualistic
63   interaction. This ecological interaction drives the convergence of warning patterns in defended species living
64   in sympatry: local predators indeed learn the association between the conspicuous colour pattern of a prey
65   and its defence (Rowland et al., 2007), therefore reducing predation rate on individuals sharing the same
66   pattern (*i.e.,* belonging to the same mimicry ring). This reduction on predation risk benefits to all the individuals
67   in the mimicry ring and depends on the density of individuals sharing the same colouration, as well as on their
68   harmfulness. As a facilitative interaction, Mullerian mimicry between sympatric species may participate in
69   shaping community structure (Chazot et al., 2014; Elias et al., 2008), and in limiting local extinction risks
70   (Boussens-Dumon & Llaurens, 2021). While mimicry was well-studied in neotropical butterflies (Bates, 1862),
71   it remains surprisingly poorly studied in wasps and bees (Hymenoptera: Aculeata) (Willadsen, 2022), although
72   these species are well-known for both their conspicuous coloration and their painful stings (Wallace, 1878). A
73   few cases of convergent evolution of colour patterns are documented in bumblebees (*e.g.,* Plowright & Owen,
74   1980; Williams, 2007) and velvet ants (*e.g.,* Wilson et al., 2012, 2015), but these cases represent only a fraction
75   of the wide variety of conspicuous patterns and painfully stinging found throughout the Aculeata clade.
76   Mullerian mimicry within and among bees and wasps is indeed probably widespread. While most models of
77   Mullerian mimicry consider equal levels of defence between the sexes, as observed in Lepidoptera, only
78   females are defended in Aculeata. This female-limited defence may play a substantial role on population
79   dynamics and may modulate the effect of Mullerian mimicry on community assembly and extinction risks in
80   Aculeata. Here, we thus develop a mathematical model to investigate the effects of warning coloration and
81   Mullerian mimicry on species co-existence in species where defences are restricted to a single sex, as observed
82   in Aculeata.

83   In most Aculeata, females escape predators because of the pain induced by their sting and by the injected
84   venom (Schmidt, 2004). The stinger in wasp and bee females may then induce a substantial difference in
85   survival between defended females and undefended males, in habitats where predators are common. The
86   relative abundance of defended females and undefended males sharing the same warning colours, whatever
87   the species they belong to, then modulates the predation risk: the proportion of attacks tends to increase
88   when the proportion of defended individuals decreases (Brower, 1960; Jones et al., 2013). However, this
89   increase crucially depends on the levels of the noxiousness (Brower, 1960; Davis Rabosky et al., 2016; Howarth
90   et al., 2004). Because of the lack of defences in males, the sex-ratio within populations of Aculeata is expected
91   to be a key factor in shaping the individual predation risk within mimetic communities.

92   The sex-ratio of bees and wasps (haplodiploid species) is linked to the fertilization of the eggs, males being
93   produced from an unfertilized egg. The sex-ratio of the offspring can be modulated by fertilized females,
94   storing sperm cells after mating and thus regulating the proportion of fertilized eggs in their progeny. Males
95   tend to be smaller than females, because size is a less important factor for male fitness (Stubblefield & Seger,
96   1994). Hence, assuming an equal investment of energy in each sex, we could observe biased sex-ratio in favour

97 of the less expensive sex, namely the males (Trivers & Hare, 1976). Although, other factors may influence the
98 sex-ratio in the progeny like seasonality, resource quality and quantity and population structure (Werren,
99 1987). Thus, the sex-ratio in the progeny produced by a female may vary between different species, depending
100 on the relative investment in son production. Such variation can have a deep influence on adult sex-ratio in
101 natural populations. Because of the sex-linked differences in defence, variations in sex-ratio in mimetic species
102 may have a deep impact on individual survival, as well as on species extinction risk within mimicry rings.
103   Furthermore, in Aculeata, male and female can either display the same colour pattern or look very
104 different, leading to important difference in individual predation risk and population dynamics. In species
105 where males exhibit the same conspicuous pattern as females, they benefit from protection against predators
106 due to mimicry towards the female signal. In contrast, striking sexual dimorphism in warning signals can be
107 observed in other species (*e.g., Dasymutilla gloriosa,* Mutillidae; *Aplochares imitator*, Pompilidae) (Pitts &
108 Sadler, 2017; Wilson et al., 2015). In these sexually-dimorphic species, males can display warning colours
109 exhibited by females from other defended species living in sympatry (Evans, 1968), resulting in Batesian
110 mimicry towards the defended species (Bates, 1862). This Dual Sex-limited Mimicry (DSLM) may have a
111 contrasted effect on community assemblages. The effect of sex-ratio, as well as of the sexual dimorphism on
112 population dynamics of mimetic species thus needs to be investigated to study the impact of these mutualistic
113 interactions on extinction risk in Aculeata.
114   Using a differential equations model, we thus explicitly modelled the population dynamics of male and
115 female populations of Aculeata assuming shared predator community and competition for resources. First,
116 using a single species model, we explored the effect of sex-ratio and female noxiousness on local extinction
117 risk. Then we built a two-species model to investigate the effect of mimicry on species persistence and co-
118 existence, by specifically focusing on the effect of variations in female noxiousness and sex-ratio in the two
119 interacting species. Finally, we explored the interaction between mimicry and sex-ratio in the species co-
120 existence when dual sex-limited mimicry occurs between sympatric species.

121   **Material & Methods**

122   To investigate the effect of mimicry on communities of sex-limited defended species, such as the Aculeata,
123 we built a deterministic model considering population dynamics of both male and female of a haplodiploid
124 species. To explore the effect of automimicry on extinction risk, we first studied a single species model. Then,
125 we used a two-species model to test for the effect of mimicry between species in either both sexes or in males
126 only (with a case of dual sex-limited mimicry). All variables and parameters used in these models are detailed
127 in Table 1.

128 **1. Model and assumptions**
129   Let F_i and M_i be the population density of females and males from the species i respectively. The changes
130 in male and female densities over time, noted dF_i/dt and dM_i/dt respectively, depend on the production of
131 offspring of each sex ($O_i^{\female}$ and $O_i^{\male}$), competition between females ($C_i^{\female}$) and adult death. Adult death is
132 composed of a basic mortality rate ($D_i^{\female}$ and $D_i^{\male}$) and a specific mortality rate caused from predation ($P_i^{\female}$ and
133 $P_i^{\male}$). We thus denote:

134 (1a) $\frac{dF_i}{dt} = O_i^{\female} + C_i^{\female} + D_i^{\female} + P_i^{\female}$
135 (1b) $\frac{dM_i}{dt} = O_i^{\male} + D_i^{\male} + P_i^{\male}$

136 with $i \in \{1,2\}$.

137 *1.1. Offspring production*
138   In order to define the sex-ratio at birth in the progeny of females, we used an increasing function bounded
139 between 0 and 1, named $\mathcal{G}$ (based on Banks et al., 2017). This function determines the proportion of daughters
140 in the offspring produced by females, depending on male proportion in the population. When the proportion
141 of males increases in the population, the relative abundance of fertilised eggs (*i.e.*, the proportion of daughters
142 in the progeny) increases too. The intensity of this relationship is modulated by a parameter h_i, which

143 modulates the investment in son versus daughter production. When $h_i = 0$, sons are infinitely less costly than
144 daughters and females produce only sons. Conversely, when h_i is high ($h_i > 10$), females produce only
145 daughters. We chose values of h_i between 1 and 5 in order to explore sex-ratio from male-biased to female-
146 biased. When the value of h_i increases, the quantity of fertilised eggs, given the proportion of males in the
147 population noted ρ_i, increases too:

148 (2) $\qquad \mathcal{G}(\rho_i, h_i) = \frac{1 - exp(-h_i \rho_i)}{1 + exp(-h_i \rho_i)}$

149 where ρ_i represents the proportion of males in the population and h_i the relative cost of producing sons in the
150 species i.
151 The variation of population density (both female and males) due to offspring production by females is:

152 (3a) $\qquad O_i^{\female} = b \times \mathcal{G}\left(\frac{M_i}{F_i + M_i}, h_i\right) \times F_i = b\mathcal{G}(\rho_i, h_i)F_i$

153 (3b) $\qquad O_i^{\male} = b \times \left(1 - \mathcal{G}\left(\frac{M_i}{F_i + M_i}, h_i\right)\right) \times F_i = b\left(1 - \mathcal{G}(\rho_i, h_i)\right)F_i$

154 where b represents the individual rate at which females reproduce.

155 *1.2. Competition within and between species*
156 Following existing models on population dynamics of mimetic species (*e.g.,* Kumazawa et al., 2006;
157 Sekimura et al., 2014; Yamauchi, 1994), we included exploitative competition in our model. We modelled
158 competition only between females because most limiting resources of food and nesting sites are sought out
159 only by females (Cane et al., 2017; Schneider et al., 2004). The effect of competition between females depends
160 on two parameters: a coefficient of niche overlap c_{ij} between species i and j, and the limiting factor of resources
161 K shared by sympatric species. When $j = i$, c_{ij} represents the strength of the intraspecific competition and we
162 assumed $c_{ii} = 1$. Because we expected niche overlap to be maximum within species, interspecific competition
163 is expected to be weaker than intraspecific one, so $c_{ij} \leq 1$. Except when explicitly mentioned, we considered c_{ij}
164 = 0.3 and $K = 1000$. The variation of female population density due to interspecific and intraspecific competition
165 for resources is then:

166 (4) $\qquad C_i^{\female} = -\frac{F_i}{K} \times \sum_{j=1}^{2} c_{ij} F_j$

167 where K represents the carrying capacity linked to local resources and c_{ij} the coefficient of niche overlap
168 between females i and j.

169 *1.3. Adult mortality*
170 Males and females suffer from basic mortality (at rate D) and a mortality caused by predation (at rate P).
171 The variation of female and male densities due to basic adult mortality are respectively:

172 (5a) $\qquad D_i^{\female} = -d \times F_i$
173 (5b) $\qquad D_i^{\male} = -d \times M_i$

174 where d is the basic death rate.
175 Survival from predation then depend on the sex of the individual, because only female possess defences.
176 The sting of female may facilitate their escape after an attack by a predator. We thus assumed that the
177 mortality rate due to predation is different between males and females, considering females have a probability
178 of escaping an attack depending on their noxiousness. Furthermore, survival from predation in both sexes can
179 be increased because of predator learning. The predation terms for females and males can thus be written as:

180 (6a) $\qquad P_i^{\female} = -\frac{p \times (1 - \alpha_i \lambda_i)}{L_i} \times F_i$ and
181 (6b) $\qquad P_i^{\male} = -\frac{p}{L_i} \times M_i$

where p is the predation rate, α_i represents the direct effect of the sting on the probability for females to escape an attack, λ_i is the noxiousness of females and L_i represents the indirect protection due to mimicry. When $\alpha_i = 0$, sting does not enhance female escaping, so that males and females have the same mortality rate due to predation.

Following Joron & Iwasa (2005) and suggested by Mallet & Joron (1999), we used a density-dependent effect of mimicry on predation. When a predator meets an unpalatable individual, it associates the noxiousness and the conspicuous pattern, reinforcing the protection provided by mimicry. As the number of unpalatable individuals sharing the same signal increases, the predation rate will decrease. Then, the predation death rate hyperbolically decreases as population size of defended prey increases. Note that this advantage against predators applies to both defended and undefended individuals (*i.e.,* in both males and females in Aculeata), as long as they share the same conspicuous coloration. Nevertheless, the relative abundance of undefended and harmful individuals sharing the same conspicuous signal, respectively males and females in Aculeata, is likely to modulate the protection brought by mimicry: the proportion of attack tends to increase when the proportion of defended individuals decreases within a mimicry ring (Brower, 1960; Jones et al., 2013). Thus, we assumed that the proportion of males in a mimicry ring had a negative effect on protection provided by mimicry, so the indirect protection due to mimicry would be:

(7)
$$L_i = 1 + \overbrace{\left(\sum_{j=1}^{2} S_{ij}\lambda_j F_j\right)}^{\substack{\text{density}-\text{dependent} \\ \text{effect of defended} \\ \text{females}}} \times \underbrace{\left(1 - \beta \frac{\sum_{j=1}^{2} S_{ij}M_j}{\sum_{j=1}^{2} S_{ij}(F_j+M_j)}\right)}_{\substack{\text{negative effect of} \\ \text{male proportion}}}$$

where λ_j is the noxiousness of female j and S_{ij} is the similarity rate of warning signals between species i and j. When $S_{ij} = 0$, there is no mimicry between individuals of species i and j while when $S_{ij} = 1$, the two species are perfect mimics (we leave aside cases of imperfect mimicry). Then β is the negative impact of harmless males on predator avoidance. When $\beta = 0$, there is no impact of undefended males on predator learning.

Finally, the variation of population density (both female and males) due to mortality caused by predation is:

(8a)
$$P_i^{\female} = -\frac{p \times (1-\alpha_i\lambda_i)}{1+\left(\sum_{j=1}^{2} S_{ij}\lambda_j F_j\right) \times \left(1-\beta\frac{\sum_{j=1}^{2} S_{ij}M_j}{\sum_{j=1}^{2} S_{ij}(F_j+M_j)}\right)} \times F_i$$

(8b)
$$P_i^{\male} = -\frac{p}{1+\left(\sum_{j=1}^{2} S_{ij}\lambda_j F_j\right) \times \left(1-\beta\frac{\sum_{j=1}^{2} S_{ij}M_j}{\sum_{j=1}^{2} S_{ij}(F_j+M_j)}\right)} \times M_i$$

By combining equations (1a), (3a), (4), (5a), (8a) and (1b), (3b), (5b), (8b) we obtain the following system of two equations:

(9a)
$$\frac{dF_i}{dt} = b\mathcal{G}\left(\frac{M_i}{F_i+M_i}, h_i\right)F_i - \frac{F_i}{K}\sum_{j=1}^{2} c_{ij}F_j - dF_i - \frac{p(1-\alpha_i\lambda_i)}{1+\left(\sum_{j=1}^{2} S_{ij}\lambda_j F_j\right) \times \left(1-\beta\frac{\sum_{j=1}^{2} S_{ij}M_j}{\sum_{j=1}^{2} S_{ij}(F_j+M_j)}\right)}F_i$$

(9b)
$$\frac{dM_i}{dt} = b\left(1 - \mathcal{G}\left(\frac{M_i}{F_i+M_i}, h_i\right)\right)F_i - dM_i - \frac{p}{1+\left(\sum_{j=1}^{2} S_{ij}\lambda_j F_j\right) \times \left(1-\beta\frac{\sum_{j=1}^{2} S_{ij}M_j}{\sum_{j=1}^{2} S_{ij}(F_j+M_j)}\right)}M_i$$

Table 1. Variable and parameters, with their signification and values.

Abbreviation	Description	Interval
Variables		
F_i	Number of females in species i	$F_i \geq 0$
M_i	Number of males in species i	$M_i \geq 0$

ρ_i	Male proportion in species i	$\rho_i \in [0,1]$

Function

$\mathcal{G}$	Function regulating sex-ratio in the offspring

Parameters

h_i	Relative investment in sons in species i	$h_i > 0$
b	Birth rate	$b \in [0.7, 1]$
d	Basic death rate	$d \in [0.1, 0.3]$
c_{ij}	Strength of the competition between females i and j	$c_{ij} = 0.3 \ (c_{ii} = 1)$
K	Carrying capacity linked to local resources	$K = 1000$
p	Predation rate on conspicuous species	$p \in [0.3, 0.7]$
λ_i	Unpalatability degree of females of species i	$\lambda_i \in [0, 0.05]$
S_{ij}	Similarity rate between species i and j	$S_{ij} = 0$ or $1 \ (S_{ii} = 1)$
α	Intensity of the direct effect of the sting	$\alpha = 5$
β	Intensity of the negative effect of males	$\beta = 0.8$

212

213 **2. Numerical simulations**

214 Except when explicitly mentioned, we randomly chose initial abundances (F_i and M_i, which fix the initial
215 male proportion ρ_i), birth rate (b), death rate (d) and predation rate (p) in each simulation, and the other
216 parameters were fixed to their default values (see Table 1). Very few ecological data are available in the
217 literature to accurately estimate the values of most parameters, and some parameters might be difficult to
218 directly measure in the wild (*e.g.,* λ, α and β). Hence, the intervals explored and the fixed values were chosen
219 based on previous exploratory simulations: we focused on parameters values enabling a large range of possible
220 outcomes (*i.e.,* values below or above these ranges force the maintenance or extinction of populations) to
221 explore a diversity of ecological scenarios. Note that the absolute values considered might depend on the
222 relationship between the parameters and the number of species studied.

223 *2.1. Exploring the effect of noxiousness and sex-ratio on extinction risks for one species*

224 In mimetic populations, the protection against predation is based on the unpalatability of defended
225 individuals and their relative abundance in the population. As a first step, we studied how these two aspects
226 influence the defence level of a mimetic population as well as their extinction risks, considering only one
227 species. From the general equations (9a) and (9b) we can write the change of female and male densities in a
228 single species by fixing $F_2 = 0$ and $M_2 = 0$. Thus, we obtain:

229 (10a) $\dfrac{dF_1}{dt} = b\mathcal{G}\left(\dfrac{M_1}{F_1+M_1}, h_1\right)F_1 - \dfrac{c_{11}F_1}{K}F_1 - dF_1 - \dfrac{p(1-\alpha\lambda_1)}{1+\lambda_1 F_1(1-\beta\rho_1)}F_1$

230 (10b) $\dfrac{dM_1}{dt} = b\left(1 - \mathcal{G}\left(\dfrac{M_1}{F_1+M_1}, h_1\right)\right)F_1 - dM_1 - \dfrac{p}{1+\lambda_1 F_1(1-\beta\rho_1)}M_1$

231 First, we explored the state of the population at equilibrium depending on predation pressure (p) on the
232 one hand, and the two main components of the group defence, *i.e.,* female noxiousness (λ) and sex-ratio (*i.e.,*
233 the proportion of defended females *vs*. harmless males, driven by the investment in sons h). Although we only
234 considered a single species, the system was difficult to study analytically because of the shape of the $\mathcal{G}$ function
235 and the different effects of competition and predation on males and females (see the mathematical detail in
236 supplementary). We therefore explored the single-species model numerically only by performing simulations
237 for different values of p within [0,1] with a step of 0.1, and different values of λ_1 within [0,0.05] with a step of
238 0.005. We recorded the state of the population at equilibrium (extinct or maintained) as well as the proportion

239 of males, for 500 simulations per combinations of p and λ_1, and this for two values of investment in sons: in
240 favour of males ($h_1 = 2$) or in favour of females ($h_1 = 5$).
241   In addition, we also observed if mortality induced by predation has an effect on sex-ratio at equilibrium or
242 if it remained constant. Thus, we performed 5000 simulations with random values of p, for 4 degrees of
243 investment in sons ($h_1 \in \{2,3,4,5\}$ with a fixed value of $\lambda_1 = 0.01$) and we recorded the male proportion at
244 equilibrium. We made linear regressions and we tested the effect of predation pressure on the proportion of
245 males at the equilibrium, using python packages *scikit-learn ver. 0.24.1* (Pedregosa et al., 2011) and *seaborn*
246 *ver. 0.11.1* (Waskom et al., 2017).
247   Furthermore, we explored the effect of the direct protection provided by the sting for females (driven by
248 α) as well as the cost of male proportion on predator learning (driven by β) on the population equilibrium.
249 These two parameters are linked to the harmfulness of females and the investment in son production, and are
250 specific to the Aculeata model. We chose values of $\lambda_1 = 0.02$ and $p = 0.6$ for which the population was
251 maintained in the first experiment, then we varied α within [0,10] with a step of 1, and β within [0,1] with a
252 step of 0.1, for random values of h_1 within [2,5]. We recorded the frequency of persistence at the equilibrium
253 for 500 simulations per combinations of α and β.

254 *2.2. Investigating the effect of mimicry between two species*
255   We investigated the effect of mimicry on co-existence of species in sympatry considering two species,
256 mimetic or not (see the detailed systems of equations S1 and S2 in supplementary). To focus on the effect of
257 mimicry, we considered females from both species as equally noxious ($\lambda_1 = \lambda_2$), and similar investment in male
258 production in both species ($h_1 = h_2$). We performed different simulations with different values of $\lambda_1 = \lambda_2$ within
259 [0.01, 0.05] using an increment of 0.005, and $h_1 = h_2$ within [1, 5] with a step of 0.5. We compared two types
260 of community: either the two species display a different warning signal (no mimicry, $S_{ij} = 0$) or both species
261 display the same warning signal (mimicry, $S_{ij} = 1$). We ran 500 simulations for each set of parameters and each
262 type of community and we recorded the equilibrium state for each species. We then calculated the frequency
263 of co-existence observed over the 500 simulations, for each combination of λ and h values.

264 *2.3. Investigating the level of mutualism between mimetic species on their co-existence*
265   Because females of mimetic species contribute to the protection against predators, we tested the impact
266 of uneven mutualistic interaction on species extinction and co-existence using unequal defence level between
267 the species ($\lambda_1 \neq \lambda_2$) and different investment in male production ($h_1 \neq h_2$).
268   First, we explored uneven female noxiousness and investment in sons separately. We performed
269 simulations with different values of λ_1 and λ_2 within [0, 0.05] with a step of 0.005, with random values of $h_1 =$
270 h_2. In the same way, we performed simulations where the values of h_1 and h_2 varied within [1, 5] with a step
271 of 0.5, with random values of $\lambda_1 = \lambda_2$. In either case, we recorded the equilibrium obtained from 500 simulations
272 per combinations of λ_1 and λ_2 (or h_1 and h_2 respectively), for each community.
273   Then, we considered unequal female noxiousness ($\lambda_1 \neq \lambda_2$) and different investment in male production (h_1
274 $\neq h_2$) at the same time. We performed simulations with different values of λ_1 and λ_2 within [0.01, 0.05] with a
275 step of 0.01, and of h_1 and h_2 within [1, 5] with a step of 1. We ran 500 simulations for each parameter set (*i.e.*,
276 combinations of λ_1, λ_2, h_1 and h_2 values) and recorded the equilibria for the two types of communities (either
277 mimetic or not). In both experiments, we considered the equilibrium state at the scale of the community:
278 either co-extinction, extinction of one species (1 or 2) or co-existence.

279 *2.4. Investigating the effect of dual sex-limited mimicry*
280   Finally, we investigated the effect of dual sex-limited mimicry, considering that species 2 display sexual
281 dimorphism in coloration, with males being mimetic to species 1. In contrast, the species 1 stayed
282 monomorphic. We thus considered a slightly different model for indirect mimetic protection, by assigning
283 different similarity rates S_{ij} for males and females:

284   (11)

$$\begin{cases} \frac{dF_1}{dt} = b\mathcal{G}(\rho_1, h_1)F_1 - \frac{F_1 + c_{12}F_2}{K}F_1 - dF_1 - \frac{p(1-\alpha\lambda_1)}{1+\lambda_1 F_1\left(1-\beta\frac{M_1+M_2}{F_1+M_1+M_2}\right)}F_1 \\[2mm] \frac{dM_1}{dt} = b\left(1 - \mathcal{G}(\rho_1, h_1)\right)F_1 - dM_1 - \frac{p}{1+\lambda_1 F_1\left(1-\beta\frac{M_1+M_2}{F_1+M_1+M_2}\right)}M_1 \\[2mm] \frac{dF_2}{dt} = b\mathcal{G}(\rho_2, h_2)F_2 - \frac{c_{21}F_1 + F_2}{K}F_2 - dF_2 - \frac{p(1-\alpha\lambda_2)}{1+\lambda_2 F_2}F_2 \\[2mm] \frac{dM_2}{dt} = b\left(1 - \mathcal{G}(\rho_2, h_2)\right)F_2 - dM_2 - \frac{p}{1+\lambda_1 F_1\left(1-\beta\frac{M_1+M_2}{F_1+M_1+M_2}\right)}M_2 \end{cases}$$

285   where $1 + \lambda_2 F_2$ is the indirect mimetic protection for females F_2 and $1 + \lambda_1 F_1\left(1 - \beta\frac{M_1+M_2}{F_1+M_1+M_2}\right)$ is the indirect
286   mimetic protection for populations F_1, M_1 and M_2.
287   With this model, we performed different simulations with different values of λ_1 and λ_2 within [0.01, 0.05]
288   with a step of 0.01, and of h_1 and h_2 within [1, 5] with a step of 1. We ran 500 simulations for each parameter
289   set (*i.e.*, combinations of λ_1, λ_2, h_1 and h_2 values) and recorded the equilibrium for the community. Because
290   female population of the species 1 has to carry the cost of the two male populations, we reduced the intensity
291   of the cost of males on predator learning by fixing β = 0.5, instead of β = 0.8.

292   **3. Running simulations**
293   Simulations were performed using Python *ver. 3.8.8* (Van Rossum & Drake, 2009) and differential equations
294   were solved using the function *odeint* from the package *Scipy ver. 1.6.2* (Virtanen et al., 2020). The scripts are
295   available on the following link: https://zenodo.org/badge/latestdoi/553618533.
296   We ran simulations during a number *n* of time intervals with Δt = 50 for each interval and a time-step of
297   0.1, which makes 500 times values per interval. Simulations were stopped when population densities varied
298   less than 10^{-4} between two time intervals. Then a population was considered extinct at equilibrium when
299   female (and male) densities were under 10^{-3}. Note that the equilibria obtained were the same when using the
300   value 10^{-6} as a threshold.
301   The data were analysed and visualised using the packages *Pandas ver. 1.2.4* (McKinney et al., 2010) and
302   *Matplotlib ver. 3.5.2* (Hunter, 2007).

303   **Results**

304   **1. Effect of female noxiousness and sex-ratio on the extinction risk for a single species**
305   Mortality from predation depends on predation pressure (*p*) and the defence level at the scale of the
306   mimetic population, which relies mainly on the proportion of females (driven by investment in sons *h*) and
307   their noxiousness (λ). First, we studied the influence of these two components on the extinction risk for a single
308   species.
309   Our simulations suggest that when the predation rate is high and the noxiousness of females is low, the
310   species goes extinct (Figure 1). When the cost of producing sons is low with respect to daughters (h_1 = 2, Figure
311   1a), the sex-ratio at equilibrium is male-biased. Extinction then occurs for lower values of predation, because
312   the low density of females limits the protection against predators. Conversely, when producing sons is more
313   costly (h_1 = 5, Figure 1b), this favours the persistence of the species, even for high predation rate or limited
314   female noxiousness (Figure 1b). Thus, a species producing a male-biased sex-ratio at birth could be more
315   sensitive to extinction by predation.

316
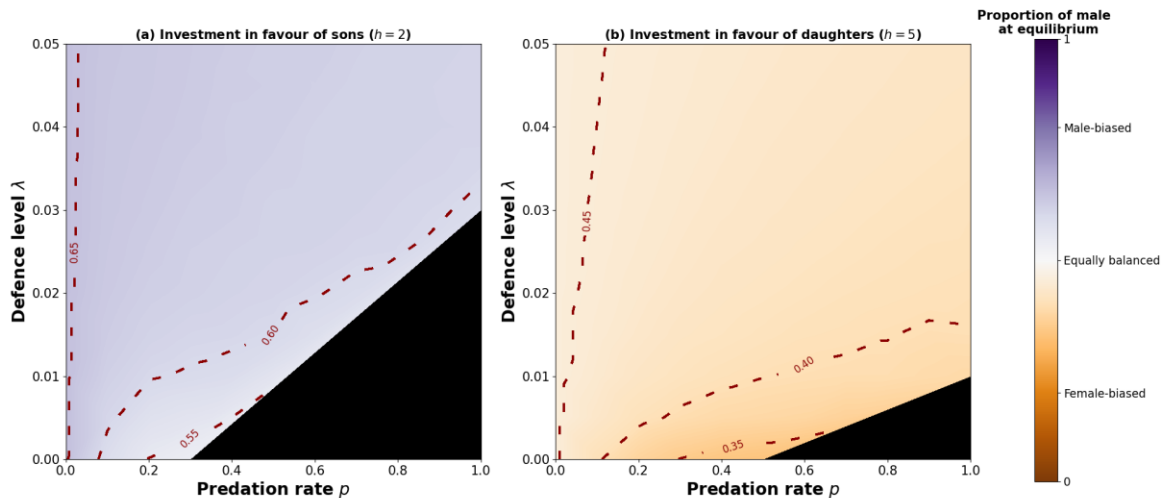
Figure 1. Effect of predation rate and female noxiousness on the persistence of the population at equilibrium, for two values of relative investment in sons: in favour of males ($h_1 = 2$, figure 1a) or in favour of females ($h_1 = 5$, figure 1b). The population is considered extinct when the equilibrium density is below 0.001 (black areas). In case of persistent population, the proportion of males at equilibrium averaged over 500 simulations is also represented: purple and orange colours indicate male and female-biased sex-ratio respectively. For each simulation, initial abundance, male proportion, birth rate, and death rate are chosen randomly and the other parameters are fixed (see Table 1).

Female noxiousness and sex-ratio both affect the defence level of the group and therefore the persistence of the mimetic population. The extinction risk is reduced when females are sufficiently noxious and abundant. The population can even be maintained if females are less numerous than males (male-biased sex-ratio), as long as they are sufficiently harmful (Figure 1a).

In addition to these two components, the presence of a stinger in females only also has an impact on extinction risk. The frequency of persistence of the population at equilibrium is lower when the cost of undefended males increases ($\beta > 0$ – Supplementary S3), but is higher when the survival advantage for females increases ($\alpha > 0$ – Supplementary S3). Thus, the group defence level in species with female-limited defences mostly relies on the noxiousness of the individuals and their abundance. Yet, the cost of undefended individuals (specific component of automimetic populations) and the female-limited survival advantage of the stinger (specific to Aculeata species) modulate this defence.

Finally, linear regressions show a significant effect of predation on the proportion of males at equilibrium (estimate for p: -0.20, $F_1^{7827} = 2082.86$, $p\text{-value} < 2.2e\text{-}16$ – Supplementary S4 and S5). The proportion of male is always lower with predation than without predation ($p = 0$ – Supplementary S4) and the sex-ratio tends to be equally balanced, even female-biased, when the predation pressure increases. When mortality increases due to higher predation rate, competition within females decreases due to fewer individuals. The increase in mortality is partly compensated by the decrease in competition, but only for females. The impact of mortality is thus relatively lower for females than for males, resulting in a diminution of male proportion.

2. Positive effect of mimicry on species co-existence

We explored the effect of mimicry between two species on their co-existence, according to their female noxiousness λ_i and relative investment in sons h_i (which drive the sex-ratio). We considered equal noxiousness ($\lambda_1 = \lambda_2$) and investment in sons ($h_1 = h_2$), and we compared a community without mimicry ($S_{ij} = 0$) and a community with mimicry ($S_{ij} = 1$).

The frequency of co-existence increases when noxiousness of females and their proportion in the offspring increase. Similarly to the single species model (Figure 1), these two components improve the defence level of the mimetic group and persistence of populations, and thus promote co-existence. However, for a given combination of $\lambda_1 = \lambda_2$ and $h_1 = h_2$, the frequency of co-existence at equilibrium is higher in the community

351 with mimicry than without mimicry. In the mimetic community, co-existence is the most frequent equilibrium
352 (observed on more than 50 % of the simulations - red line, Figure 2b) for smaller values of $\lambda_1 = \lambda_2$ and $h_1 = h_2$
353 than in the community without mimicry (Figure 2a). When the two species are strongly male-biased (*i.e.,* when
354 females are more costly than males to produce: $h_i = 1$, Figure 2), or when females are poorly noxious it
355 increases the frequency of co-extinction.
356   For a mimetic population or community to persist, it requires a minimum group defence level which mainly
357 depends on female noxiousness and their abundance in the population. Considering equally harmful females
358 in the two species, mimicry thus favours co-existence by increasing the abundance of defended individuals in
359 the mimetic community.
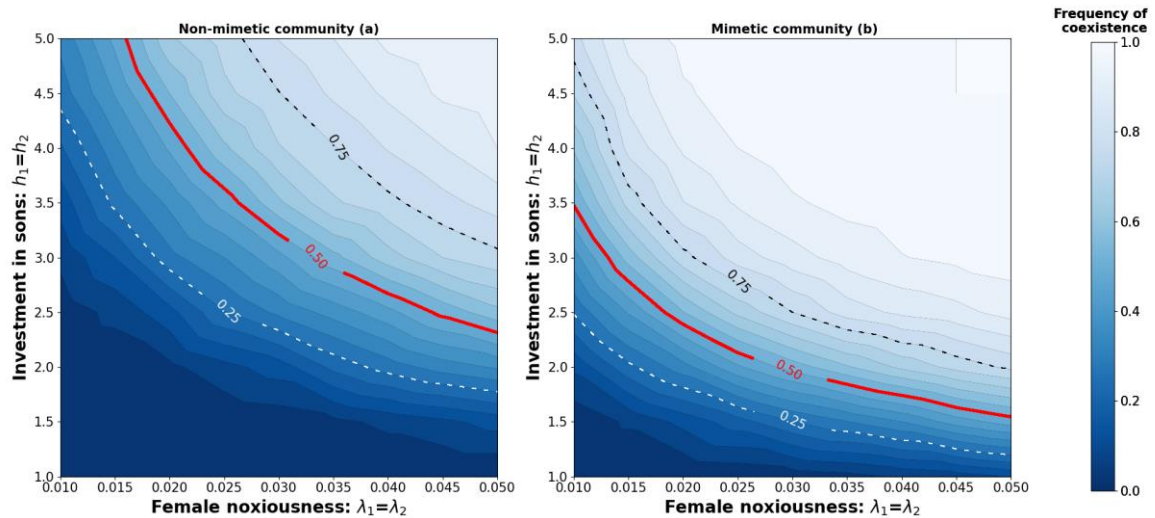
360

361   **Figure 2.** Effect of equal noxiousness and equal sex-ratio on the frequency of co-existence, for a community
362 without mimicry (left side - Figure 2a) or with mimicry between species (right side - Figure 2b). The blue
363 gradient represents the frequency of co-existence for 500 simulations. For each simulation, initial abundances,
364 male proportions, birth rate, death rate and predation rate are chosen randomly and the other parameters
365 are fixed (see Table 1). Lines represent equal levels of frequency: 50% for the red line, 25% for the light dotted
366 line and 75% for the dark dotted line.

3. Effect of uneven noxiousness and sex-ratio on the benefit of mimicry

368   Without mimicry, persistence of a species depends only on the noxiousness and relative abundance of
369 their respective females. Co-existence is thus observed when both species populations have highly harmful
370 females (high λ_i values - Figure 3b) and a low proportion of males (high h_i values - Figure 3c). When a species
371 produces relatively more females and they are better defended than the other species, the most frequently
372 observed equilibrium is the exclusion of the less protected species (purple and grey areas - Figure 3a). Co-
373 extinction occurs when either a species has more females but poorly noxious, or the opposite (blue areas -
374 Figure 3a).
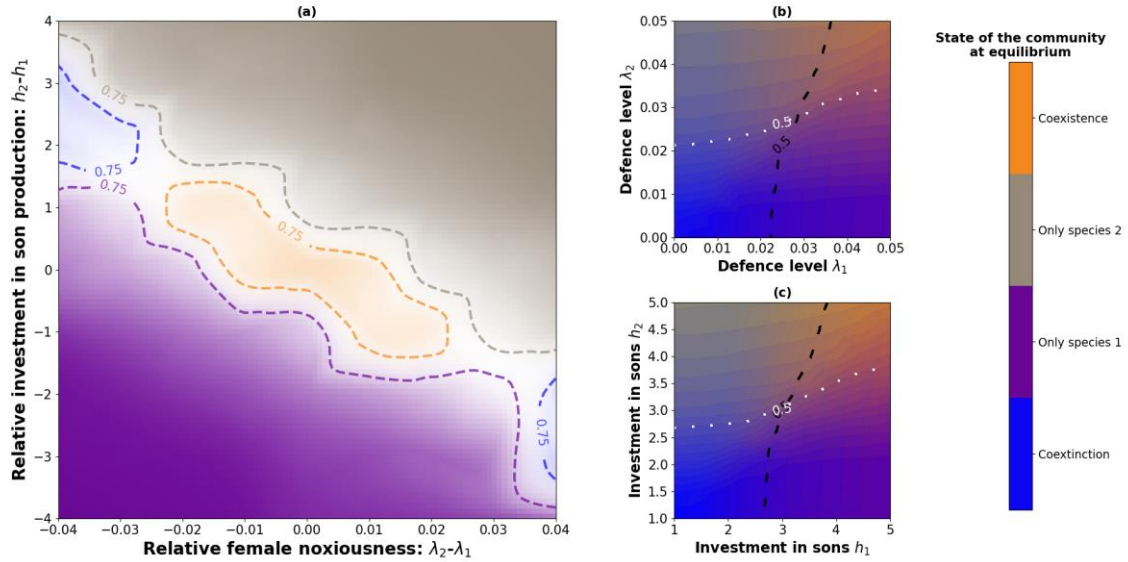
375

Figure 3. Effect of unequal female noxiousness and unequal investment in sons on the species co-existence for a non-mimetic community. We consider 4 equilibria: co-extinction (blue), co-existence (orange), only species 1 (purple) or only species 2 (grey). The colour gradient represents the frequency of equilibria for 500 simulations. In Figure 3a, because multiple pairs of parameters values may lead to the same value of $\lambda_2 - \lambda_1$ or $h_2 - h_1$, transparency levels match with the frequency of the most frequently observed equilibrium (full transparency corresponds to a frequency of 25% or under). For each simulation, initial abundances, male proportions, birth rate, death rate and predation rate are chosen randomly and the other parameters are fixed (see Table 1). Equal defence levels or sex-ratio are also randomly chosen when they are not plotted (for Figure 3b and 3c). The black and white lines represent the limit of 50% observed persistence, respectively for species 1 and 2.

When species are mimetic, the co-existence occurs as soon as a one species out of the two species is sufficiently protected (Figure 4a), either because their females are harmful (high λ_i values - Figure 4b) or relatively abundant (high h_i values promoting female-biased sex-ratio - Figure 4d). Harmless mimetic species can even be maintained ($\lambda_i = 0$), when the other species has very noxious females (Batesian mimicry). We see that co-existence occurs for most values of λ_1, λ_2, h_1 and h_2 (orange area, Figure 4). Species exclusion is still observed when the difference of investment in sons is important ($\Delta h = 4$ or -4 – Figure 4a) because the difference of female densities between the two species leads to competitive exclusion. Hence, mimicry favours co-existence in female-limited defence, even with unbalanced species traits
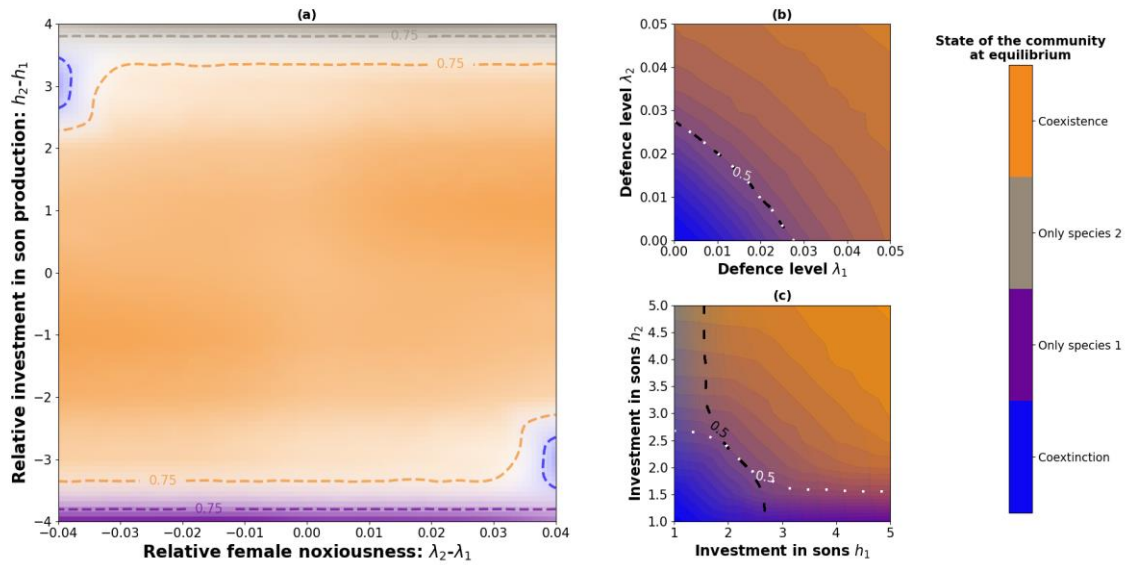
Figure 4. Effect of unequal female noxiousness and unequal investment in sons on the species co-existence for a mimetic community. We consider 4 equilibria: co-extinction (blue), co-existence (orange), only species 1 (purple) or only species 2 (grey). The colour gradient represents the frequency of equilibria for 500 simulations. In Figure 4a, because multiple pairs of parameters values may lead to the same value of $\lambda_2 - \lambda_1$ or $h_2 - h_1$, transparency levels match with the frequency of the most frequently observed equilibrium (full transparency corresponds to a frequency of 25% or under). For each simulation, initial abundances, male proportions, birth rate, death rate and predation rate are chosen randomly and the other parameters are fixed (see Table 1). Equal defence levels or sex-ratio are also randomly chosen when they are not plotted (for Figure 4b and 4c). The black and white lines represent the limit of 50% observed persistence, respectively for species 1 and 2.

**4. Effect of dual sex-limited mimicry on co-existence**

Finally, we explore the effect of dual sex-limited mimicry (DSLM) on species co-existence, considering the species 1 as monomorphic and the species 2 as dimorphic.

Our simulations show that species co-existence is frequent only in a restricted range of relative female noxiousness (*-0.04 < Δλ < 0.02* – Figure 5) and investment in sons (*-2.5 < Δh < 1.5* – Figure 5). These values correspond to situations where the monomorphic species is relatively better protected than the dimorphic species, either with more noxious and/or more abundant females (orange area – Figure 5).

However, when both species have similar protections, the most frequent equilibrium is co-extinction. In these situations, females of the monomorphic species are not sufficiently protected from predation due to the cost of undefended males, leading to their extinction. Because males of the dimorphic species are no longer protected and cannot maintain themselves, the female population of this species will decrease until there are not enough defended individuals to ensure the protection of the colour pattern, leading to the extinction of the second species (blue area – Figure 5).

Considering dual sex-limited mimicry, females of the two species do not share the same aposematic pattern and therefore only interact negatively through competition. When a female population is better protected than the other one, this leads to species exclusion (purple and grey areas – Figure 5). The second species may persist without the other species protecting its males if dimorphic females are protected enough to survive despite the decrease of their population.

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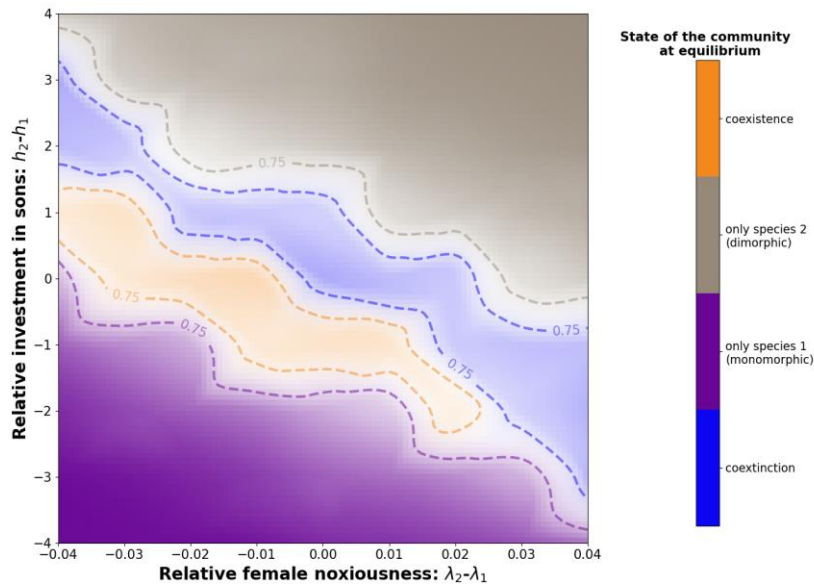
Figure 5. Effect of unequal female noxiousness and unequal investment in sons on the species co-existence, considering a monomorphic species (species 1) and a dimorphic species (species 2). Males of the second species mimic individuals of the species 1, while females are aposematic but with a distinct colour pattern. We consider 4 equilibria: co-extinction (blue), co-existence (orange), only species 1 (purple) and only species 2 (grey). Colour represents the most frequently observed equilibrium for 500 simulations. Because multiple pairs of parameters values may lead to the same value of $\lambda_2 - \lambda_1$ or $h_2 - h_1$, transparency levels match with the frequency of the equilibrium (full transparency corresponds to a frequency of 25% or under). For each simulation, initial abundances, male proportions, birth rate, death rate and predation rate are chosen randomly, the other parameters are fixed at their default value (see Table 1) except $\beta = 0.5$ in order to reduce the cost of males. Colored lines represent equal levels of frequency.

With a non-mimetic community, similar group defence levels between the two mimetic populations promote co-existence (Figure 3), but favour co-extinction when we consider a case of dual sex-limited mimicry (Figure 5). Instead, co-existence occurs when group defences levels are asymmetrical between the two populations and in favour of the monomorphic species, which carries the cost of all undefended males. Moreover, the co-existence is much less frequent in the community with dual sex-limited mimicry than with symmetric mimicry between the two species (Figure 4). Thus, dual sex-limited mimicry increases the risks of co-extinction, especially when both species have the same level of group defence. Under these conditions, co-existence requires a lower level of defence in the dimorphic species. In the absence of males mimicking females from species 2, limited abundance of species 2 reduces competition with species 1 females, and favour co-existence. Note that we reduced the cost of males on predator learning for these simulations ($\beta = 0.5$). With a value of $\beta = 0.8$, co-existence is frequent only when $\Delta\lambda = -0.01$ and $\Delta h = -1$, so only when the monomorphic is slightly better protected than the other one.

Discussion

In this paper, we provided a mathematical model for population dynamics of Mullerian mimetic species with female-limited defences, considering mimetic interaction between two species. Our findings are relevant to identify important ecological factors impacting the extinction risk in Aculeata communities.

1. Sex-ratio and extinction risk in Aculeata: the threat of male automimicry

Our model first considered the population dynamics in one haplodiploid aposematic species, where only females have defences and males act as Batesian mimics, specific to Aculeata. Our results showed that the resistance of such a species to an increasing predation pressure was related to two different components: the noxiousness of females, and the sex-ratio in the population. Our model highlighted the effect of the cost of investment in sons on the extinction risk in species with female-limited defence such as Aculeata species. Our

455 results showed that for a fixed level of female noxiousness, the probability of extinction increases as the
456 proportion of male increases in the population, when females are rarer than males (male-biased sex-ratio).
457 Previous theoretical studies on Batesian mimicry complexes showed that the relative frequency of the mimics
458 is correlated with the probability of a predator attack, when the model individuals are rarer than the mimics
459 (Huheey, 1964; Holling, 1965; Emlen, 1968), and these results were supported by empirical studies (Lindström
460 et al., 1997; Brower, 1960). However, the link between extinction risk and sex-ratio also depends on the level
461 of unpalatability in females, which is consistent with the empirical (Lindström et al., 1997; Brower, 1960;
462 Nonacs, 1985) and theoretical literature (Brower et al., 1970). Indeed, in Batesian mimicry, palatable mimics
463 can be abundant when the level of noxiousness in the model species is high (Brower, 1960; Brower et al.,
464 1970).
465   In solitary wasp and bee species, strongly male-biased, sex-ratio can be observed. Trivers & Hare (1976)
466 indeed found male-biased sex-ratio for solitary wasps and bees from natural nests, bumblebees (*from* Webb,
467 1961 *in* Trivers & Hare, 1976) and some solitary species from trap nests (*from* Krombein, 1967 *in* Trivers &
468 Hare, 1976), with sex-ratios with even more than two males per female in some species. Significant proportion
469 of automimics have been reported by Brower (1969) in populations of the monarch butterfly *Danaus plexippus*
470 (Lepidoptera)*,* suggesting that important proportion of harmless individuals within population does not
471 prevent the persistence of aposematic species in the wild.
472   The negative effect of males on the protection against predators can be reduced in species with sexually-
473 differentiated phenology. In some Aculeata species, males come out after females during the season and
474 therefore most predators have already learnt the aposematic signal. Waldbauer & Sheldon (1971) observed
475 the phenology of Aculeata and of their insectivorous bird predators in a temperate area of the USA. The
476 fledging of young birds mostly occurred during Summer and simultaneously with the abundance peak of
477 Aculeata models, so the majority of naïve predator learning occurs during this period. Moreover, they also
478 observed that stingless males were scarce in Aculeata populations during the summer and abundant in spring
479 and fall. Longair (1981) and Seger (1983) both noted variations in the sex-ratio between the two generations
480 of most bivoltine species of bees and wasps from temperate areas. The sex-ratio was balanced or female-
481 biased for the summer generation, but becomes male-biased for the overwinter generation.
482   These empirical observations suggest that the lack of defence in aculeate males can influence population
483 dynamics and may have influenced the evolution of investment in male offspring throughout the year. Thus,
484 the extinction risk in Aculeata might depend on the variations of their sex-ratio through time in the different
485 species, but also on their resemblance with other defended species living in sympatry.

486 **2. Mimicry as a mutualistic interaction limiting extinction**
487   Our results confirmed the positive effect of mimicry on species co-existence, despite the negative effects
488 of undefended mimetic males and of the competition between females. Our model suggests that species co-
489 existence depends on the level of noxiousness of females and on their proportion in the natural communities
490 of mimetic species. Co-existence between two mimetic species may indeed occur when the level of defence
491 of females from one species is sufficiently high, even if defences are lacking in the other species (*i.e.* Batesian
492 mimicry).
493   Our results demonstrated the co-existence of mimetic species despite inter-specific competition. Co-
494 mimetic species are found in sympatry, because the convergence evolution of warning coloration is promoted
495 by the behaviour of the local predators feeding on these different aposematic species. Co-mimetic species
496 therefore have largely overlapping ecological niches (Elias et al., 2008) and may thus often compete for
497 resources. Interspecific competition tends to reduce species richness, but other ecological interactions have
498 been documented to mediate the intensity of the competition. Models of foodweb indeed have shown that
499 predation may reduce competition between prey (Droosel et al., 2001) and using a mathematical resource-
500 consumer model, Gross (2008) has shown that positive interaction among exploitative competitors may
501 enhance coexistence between species despite a net negative effect of interspecific interactions. For instance,
502 co-existence in plant communities can be favoured through interactions that facilitate nutrient supply, either
503 between plant species (Bertness & Leonard, 1997), *via* mycorrhizal interactions (Bergelson & Crawley, 1988)
504 or through the effect of herbivores (Jensen & Nielsen, 1986). Our model highlights the mitigating effect of
505 another mutualistic interaction, namely Mullerian mimicry, on the competitive exclusion between species
506 arising from female competition for resources. Such a mitigating effect of Mullerian mimicry on species
507 extinction risk was recently described in a previous model where equal level of defences were assumed across

sexes (Boussens-Dumon & Llaurens, 2021). Our model demonstrates that, even when some mimetic individuals are unequally defended and therefore do not participate equitably in the predator education, Mullerian mimicry can still limit species exclusion caused by competition.

Our model considered the interaction between two species only, but natural communities of mimetic wasps and bees are composed of multiple species, occupy large geographical areas, and also interact with Batesian mimics. For instance, velvet ants and bumble bees are known to form large mimicry rings, in terms of number of species and geographical distributions (Hines et al., 2017; Wilson et al., 2015). Some conspicuous colour patterns are also widespread among Aculeata, and their persistence in large number of species might be promote by the positive effects of mimicry. The black-and-yellow pattern and the black-orange-black pattern are two common colourations among Aculeata and Hymenoptera in general (Boppré et al., 2016; Mora & Henson, 2019). Wasps and bees colour patterns occur also in other taxa of insects including undefended species like flies of the family Syrphidae (Leavey et al., 2021; Waldbauer, 1970). Thus, the protection provided by mimetic interaction involving Aculeata could benefit a large number of species and limit their extinction risk.

Mimicry between wasps and bees is a relevant factor to better understand the population dynamics and co-existence of Aculeata species. More broadly, since Aculeata are important pollinators, as are some of their Batesian mimics such as hoverflies (Syrphidae; Doyle et al., 2020), the positive effect of mimicry on co-existence could be even more important to consider given the current decline in pollinator populations (Biesmeijer et al., 2006; Hallman et al., 2017).

3. Male-limited mimicry as a destabilising factor in Aculeata communities

While our model generally suggests a positive effect of mimicry on species co-existence in Aculeata communities, the specific case of dual sex-limited mimicry (Evans, 1968) provides more contrasted result. In our model, the dual sex-limited mimicry (DSLM), where harmless males from a sexually dimorphic species resemble to defended females from another species, tends to increase the risks of co-extinction. Co-existence is indeed predicted in only a restricted range of female noxiousness and investment in sons: the monomorphic species mimicked by males from the other species needs to be relatively more protected than the dimorphic species, either with females more defended or more abundant, in order to maintain a sufficient level of protection, despite the cost of the additional mimetic males on the warning signal.

In Aculeata, DSLM was described in a few species of Pompilidae (Evans, 1968; Pitts & Sadler, 2017) and Mutillidae (Wilson et al., 2015). Other cases of DSLM may occur in Aculeata, especially for the mutilid wasps where the extreme sexual dimorphism probably prevent generalization of warning signals displayed by males and females (Pilgrim & Pitts, 2006). The evolution of colour dimorphism have been suggested to stem from behavioural differences between sexes (Heal, 1981; Van-Wright, 1971) and/or microhabitat divergence between male and female, resulting in contrasted selective pressures acting on either sexes. For instance, in the genus *Chirodamus* (Pompilidae), females hunt spiders on the ground like other wasp species including *Pepsis sp.*, while males spend many times flying among social wasp workers (Ewans, 1968). In mutilid wasps, all females are apterous, while males do have wings and may have wider distribution areas and share the environment with other species. In wasps and bees, the obligatory sexual dimorphism in defences might also contribute to contrasted selection acting on male and female coloration and influence the evolution of dual sex-limited mimicry.

Our results highlight the impact of dual sex-limited mimicry on co-existence in Aculeata species. Undefended males are likely to represent a cost and might increase the extinction risk of the population, especially in species with poorly defended females or with a male-biased sex-ratio. In case of DSLM, species co-existence might stem from a precarious equilibrium so that anthropic pressures disturbing natural population dynamics of wasps and bees might have an even more significant effect on extinction risk than in other cases of mimicry between monomorphic species.

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Data, scripts, code, and supplementary information availability

Scripts and code are available online: https://zenodo.org/badge/latestdoi/553618533.

Conflict of interest disclosure

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758

759 (S1)

$$\begin{cases} \frac{dF_1}{dt} = b\mathcal{G}(\rho_1, h_1)F_1 - \frac{F_1 + c_{12}F_2}{K}F_1 - dF_1 - \frac{p(1-\alpha\lambda_1)}{1+\lambda_1 F_1\left(1-\beta\frac{M_1}{F_1+M_1}\right)}F_1 \\ \frac{dM_1}{dt} = b\left(1 - \mathcal{G}(\rho_1, h_1)\right)F_1 - dM_1 - \frac{p}{1+\lambda_1 F_1\left(1-\beta\frac{M_1}{F_1+M_1}\right)}M_1 \\ \frac{dF_2}{dt} = b\mathcal{G}(\rho_2, h_2)F_2 - \frac{c_{21}F_1 + F_2}{K}F_2 - dF_2 - \frac{p(1-\alpha\lambda_2)}{1+\lambda_2 F_2\left(1-\beta\frac{M_2}{F_2+M_2}\right)}F_2 \\ \frac{dM_2}{dt} = b\left(1 - \mathcal{G}(\rho_2, h_2)\right)F_2 - dM_2 - \frac{p}{1+\lambda_2 F_2\left(1-\beta\frac{M_2}{F_2+M_2}\right)}M_2 \end{cases}$$

760 **S1. System of equations for the non-mimetic community**, with $c_{11} = 1$, $c_{22} = 1$, $S_{11} = 1$, $S_{12} = 0$, $S_{21} = 0$ and $S_{22} =$
761 *1.*

762 (S2)

$$\begin{cases} \frac{dF_1}{dt} = b\mathcal{G}(\rho_1, h_1)F_1 - \frac{F_1 + c_{12}F_2}{K}F_1 - dF_1 - \frac{p(1-\alpha\lambda_1)}{1+(\lambda_1 F_1 + \lambda_2 F_2)\times\left(1-\beta\frac{M_1+M_2}{F_1+M_1+F_2+M_2}\right)}F_1 \\ \frac{dM_1}{dt} = b\left(1 - \mathcal{G}(\rho_1, h_1)\right)F_1 - dM_1 - \frac{p}{1+(\lambda_1 F_1 + \lambda_2 F_2)\times\left(1-\beta\frac{M_1+M_2}{F_1+M_1+F_2+M_2}\right)}M_1 \\ \frac{dF_2}{dt} = b\mathcal{G}(\rho_2, h_2)F_2 - \frac{c_{21}F_1 + F_2}{K}F_2 - dF_2 - \frac{p(1-\alpha\lambda_2)}{1+(\lambda_1 F_1 + \lambda_2 F_2)\times\left(1-\beta\frac{M_1+M_2}{F_1+M_1+F_2+M_2}\right)}F_2 \\ \frac{dM_2}{dt} = b\left(1 - \mathcal{G}(\rho_2, h_2)\right)F_2 - dM_2 - \frac{p}{1+(\lambda_1 F_1 + \lambda_2 F_2)\times\left(1-\beta\frac{M_1+M_2}{F_1+M_1+F_2+M_2}\right)}M_2 \end{cases}$$

763 **S2. System of equations for the mimetic community**, with $c_{11} = 1$, $c_{22} = 1$, $S_{11} = 1$, $S_{12} = 1$, $S_{21} = 1$ and $S_{22} = 1$.
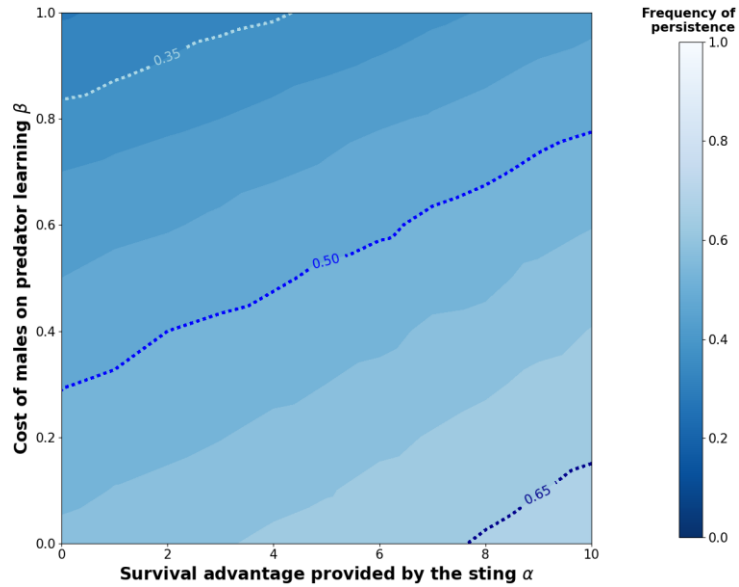
764

765 **S3**. **Effect of the female-limited survival advantage of the sting and of the cost of undefended males on the**
766 **equilibrium.** Simulations were run assuming $\lambda_1 = 0.02$ and $p = 0.6$. These parameter values insured the
767 persistence of the population (see Figure 1). The frequency of persistence was averaged over 500 simulations,
768 with random values of h_1 within [2,5] for each simulation. Moreover, initial abundance, male proportion, birth
769 rate, and death rate are chosen randomly and the other parameters are fixed (see Table 1). Blue dotted lines
770 indicate equal levels of frequency (0.35, 0.5 and 0.65).

771
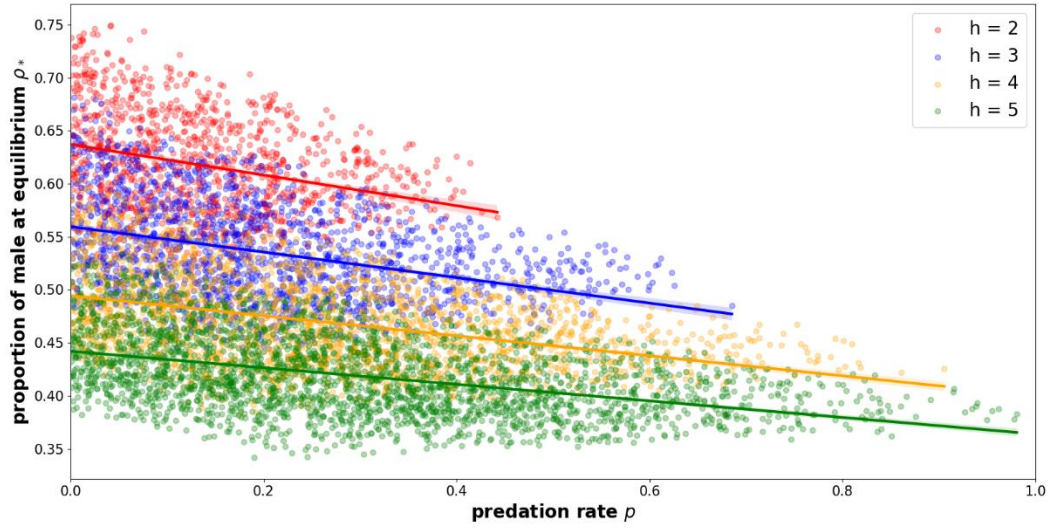
S4. Effect of predation rate on male proportion at equilibrium, for different values of *h*. We made 5000 simulations for each value of *h*, with random values of p and a fixed value of *λ = 0.01*. Simulations leading to the extinction of the population are not represented. Moreover, initial abundance, male proportion, birth rate and death rate are chosen randomly and the other parameters are fixed (see Table 1).

Values of h	Estimate for p	F-statistic	p-value
h = 2	**-0.14**	$F_1^{1132} = 104.93$	< 2.2e-16
h = 3	**-0.12**	$F_1^{1709} = 278.95$	< 2.2e-16
h = 4	**-0.09**	$F_1^{2263} = 465.24$	< 2.2e-16
h = 5	**-0.08**	$F_1^{2723} = 670.53$	< 2.2e-16
All included	**-0.20**	$F_1^{7827} = 2082.86$	< 2.2e-16

S5. Effect of predation rate on male proportion at equilibrium for one species. We made 5000 simulations for each value of *h*, with random values of p and a fixed value of *λ = 0.01*. Simulations leading to the extinction of the population are not represented. Moreover, initial abundance, male proportion, birth rate and death rate are chosen randomly and the other parameters are fixed (see Table 1). Linear regressions were performed using python packages *scikit-learn ver. 0.24.1* (Pedregosa et al., 2011) and *seaborn ver. 0.11.1* (Waskom et al., 2017).

S6. Study of the system (10a) and (10b)

We would like to stress that even if the dynamical system has only two coordinates, it is highly nonlinear and therefore difficult to study theoretically. The main difficulty derives from the function $\mathcal{G}$ appearing in birth rate, and the different effects on males and females of competition and predation.

Let us recall that the system describes the dynamics of $F(t), M(t)$ the density of females and males and depends on the male ratio $\rho(t) = M(t)/(F(t) + M(t))$. The dynamical system writes

(1) $\qquad \frac{d}{dt}F = F\left(b\mathcal{G}(\rho) - d - \frac{c}{K}F - p(\rho, F)(1 - \alpha\lambda)F\right)$

(2) $\qquad \frac{d}{dt}M = F\left(b(1 - \mathcal{G}(\rho)) - d - p(\rho, F)M\right)$

where $p(\rho, F) = \frac{p}{1 + \lambda F(1 - \beta\rho)}$.

We aim at characterizing the positive equilibria (F^*, M^*) of the system when it exists. Here we will actually compute F^* and $\rho^* = M^*/(F^* + M^*)$, and we can then retrieve $M^* = \rho^*F^*/(1 - \rho^*)$.

By considering the total population size, we obtain that at equilibrium

794   (3) $$bF + d(F + M) - \frac{c}{K}F^2 - p(F, \rho)(F + M - \alpha\lambda F) = 0$$

795   which leads dividing by $(F + M)$

796   (4) $$b(1 - \rho) - d - \frac{c}{K}F(1 - \rho) - p(F, \rho)\big(1 - \alpha\lambda(1 - \rho)\big) = 0.$$

797   and thus

798   (5) $$p(F, \rho) = \frac{b(1 - \rho) - d - \frac{c}{K}F(1 - \rho)}{1 - \alpha\lambda(1 - \rho)}.$$

799   therefore

800   (6) $$\frac{p}{1 + \lambda F(1 - \beta\rho)} = \frac{b(1 - \rho) - d - \frac{c}{K}F(1 - \rho)}{1 - \alpha\lambda(1 - \rho)}.$$

801   Using (5) in (1) we deduce that at equilibrium

802   (7) $$b\mathcal{G}(\rho) - d - \frac{c}{K}F - \frac{b(1 - \rho) - d - \frac{c}{K}F(1 - \rho)}{1 - \alpha\lambda(1 - \rho)}(1 - \alpha\lambda) = 0$$

803   which reads

804   (8) $$b\mathcal{G}(\rho) - d\frac{\alpha\lambda\rho}{1 - \alpha\lambda(1 - \rho)} - \frac{c}{K}F\left(1 - (1 - \rho)\frac{\alpha\lambda\rho}{1 - \alpha\lambda(1 - \rho)}\right) = 0$$

805   This allows to obtain F^* as a function of ρ^*

806   (9) $$F^* = \frac{b\mathcal{G}(\rho^*) - d\frac{\alpha\lambda\rho^*}{1 - \alpha\lambda(1 - \rho^*)}}{\frac{c}{K}\left(1 - (1 - \rho^*)\frac{\alpha\lambda\rho^*}{1 - \alpha\lambda(1 - \rho^*)}\right)}$$

807   We can then replace F^* in (6) and obtain that ρ^* is a solution of

808   (10) $$\frac{p}{1 + \lambda F^*(1 - \beta\rho^*)} = \frac{b(1 - \rho^*) - d - \frac{c}{K}F^*(1 - \rho^*)}{1 - \alpha\lambda(1 - \rho^*)}.$$

809 We see here, that due to the function $\mathcal{G}$ involved, and the non-linearity, an explicit expression for ρ^* is not
810 available. Moreover, it is difficult to ensure that a solution ρ^* actually exists in $(0,1)$ and that it gives a positive
811 F^* in (9).