Uncovering the effects of Müllerian mimicry on the evolution of conspicuousness in colour patterns

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Abstract

The conspicuousness of colour pattern in defended species associates with a high detectability by predators, making its evolution puzzling. Müllerian mimicry, the convergence of warning coloration among defended prey species, is pervasive in communities of conspicuous prey, and mimicry switches, with mutant individuals having the same colour pattern as other co-mimetic species, may often associate with changes in conspicuousness. Yet, the implication of mimicry for the evolution of conspicuousness has not been considered. Here, we build a model describing the population dynamics of conspicuous defended prey to explore the invasion conditions of mutants that differ from other individuals by their conspicuousness. We assume that predation risk depends not only on the number of individuals sharing a given colour pattern within the population but also on the presence of co-mimetic species. We compare the evolutionary fates of mutant colour patterns (1) that are similar to the ancestral colour pattern and thus belong to the same mimicry ring (assemblage of co-mimetic species), or (2) that are different from the ancestral colour pattern and thus potentially belong to a distinct mimicry ring. Our analytical derivations show that (1) less conspicuous colour patterns are more likely to be selected within mimicry ring, and that (2) a mimicry switch lowering predation risk can promote the invasion of a more conspicuous colour pattern. We thus highlight that the variation in conspicuousness observed in the wild results not only from the characteristics of the colour pattern (detectability, salience) but also from the local composition of mimetic communities.

INTRODUCTION

The evolution of warning colour patterns in defended species is puzzling because conspicuousness, determining the detectability of prey by predators, associates with multiple costs (Ruxton, 2019). First, individuals may have a reduced fitness incurred by metabolic cost of pigmentation (Hill, 1996; McGraw *et al.*, 2005). Second, individuals may suffer from increased attack risk by naive predators stemming from higher detectability of their more conspicuous colour patterns (Arias *et al.*, 2019).

Although higher conspicuousness entails higher detectability and therefore increased predation risk, it also associates with direct benefits. When detected, conspicuous colour patterns may be less attacked than cryptic colour patterns (often displayed by profitable prey) (Sillén-Tullberg, 1985) because of innate aversion of predators for conspicuous colour (Lindström *et al.*, 2001), diet conservatism (Marples *et al.*, 2005) or neophobia (Marples & Kelly, 1999; Aubier & Sherratt, 2015).

Conspicuousness of colour patterns also associates with indirect benefits, mediated by the learning behaviour of predators. When predators learn to avoid defended prey exhibiting warning colour patterns, higher conspicuousness can trigger more rapid avoidance-learning due to higher memorability (Roper & Redston, 1987; Ham *et al.*, 2006; Siddall & Marples, 2008). The salience of the colour pattern (i. e., the memorability and avoidance learning triggered by the colour pattern's conspicuousness), may thus facilitate the evolution of conspicuousness. Salience associated with a given colour pattern may stem from a characteristic element only, either the pattern and/or the colour that may promote recognition, learning and memorability of the defended prey by predators. For instance, typical snake zig zag pattern (Wüster *et al.*, 2004; Valkonen *et al.*, 2011) or the stripes of artificial prey (Barnett *et al.*, 2016) have been shown to contribute more than colouration to salience. In other documented cases, colour pattern is the

preponderant salient element over particular pattern (Aronsson & Gamberale-Stille, 2009), with some colours being more salient than others (Lindstedt *et al.*, 2011; Buechel *et al.*, 2018).

The implication of the local prey communities in the evolution of conspicuousness has not been formally investigated. Yet, colour patterns are often shared by several sympatric defended species, a phenomenon referred to as Müllerian mimicry (Müller, 1879). By displaying a given colour pattern, prey individuals gain protection that depends on the local abundance of their mimicry ring (i. e., the sympatric assemblage of several species sharing the same colour pattern). Indeed, when experiencing the defences of a prey belonging to a given mimicry ring, predators then avoid any prey from that mimicry ring. The protection gained depends on the level of resemblance of the pattern displayed within species to the corresponding mimicry ring and the generalisation behaviour of predators. A colour pattern with a different level of conspicuousness can then be perceived as different by predators, thereby increasing predation risk, thereby increasing predation risk (Greenwood *et al.*, 1989; Lindstrom *et al.*, 2001). By contrast, the evolution of conspicuousness of colour pattern within species might be facilitated when it associates with a switch to a mimicry ring increasing protection against predators.

Here, we use a theoretical approach to investigate the invasion conditions of a mutant colour pattern differing from the ancestral colour pattern by its conspicuousness, in a defended species engaged in Müllerian mimicry. We investigate whether a mutant colour pattern that is more conspicuous can invade when it also associates with a switch to an alternative mimicry ring. To single out the effect of mimetic environment on the evolution of conspicuousness, we deliberately consider a ‘worst case scenario’ where there is no direct benefit associated with conspicuousness (e.g., no innate aversion against conspicuousness).

Our model involves one species with wild-type and mutant individuals with different levels of conspicuousness. We consider that the mutant colour pattern belongs to either 1) the

same mimicry ring as the wild type (‘*one mimicry ring* hypothesis’: wild-type and mutant have different levels of conspicuousness but still share the same colour pattern), or 2) another mimicry ring than the wild-type (‘*two mimicry ring* hypothesis’: wild-type and mutant have different levels of conspicuousness and are perceived by predators as distinct). Under the 'two mimicry ring hypothesis', the mutant colour pattern may match another mimicry ring, and may therefore benefit from a different level of protection provided by predator avoidance learning. We thus investigate how mimetic interactions may contribute to the evolution of conspicuousness.

MATERIAL AND METHODS

General model

Using ordinary differential equations, we model the population dynamics of a conspicuous defended prey species. This focal species is composed of individuals all harbouring the same level of defence u (hereafter we treat the defence as toxins, and ‘u’ stands for unpalatability; see Tab. 1 for a summary of notations) and displaying a conspicuous colour pattern. Each individual can either display the *wild-type* phenotype (hereafter referred to using the subscript ‘*wt*’) or the *mutant* phenotype (referred to using the subscript ‘*m*’). Individuals with wild-type and mutant phenotypes can differ in the conspicuousness level of their colour pattern (c_{wt} and c_m respectively), leading to different predation risk ($p \times c_{wt}$ and $p \times c_m$, with p being the baseline predation rate; see below). The changes through time in densities N_{wt} and N_m of individuals displaying the wild-type and mutant colour patterns follow:

$$\frac{dN_{wt}}{dt} = R_{wt} + P_{wt} \qquad [1],$$

$$\frac{dN_m}{dt} = R_m + P_m \qquad [2],$$

These differential equations include terms describing local demography given by $(R_{wt}; R_m)$ and predation terms given by $(P_{wt}; P_m)$ that we now describe.

Local demography

Individuals displaying the wild-type and mutant colour pattern belong to the same species. As such, they have equal baseline growth rate *r*, compete for the same resources and share the same carrying capacity *K*. The changes in density of individuals displaying either the wild type or mutant colour pattern due to local competition are chosen as logistic regulation rules:

$$R_{wt} = rN_{wt}\left(1 - \frac{N_{wt}+N_m}{K}\right) \qquad [3],$$

$$R_m = rN_m\left(1 - \frac{N_{wt}+N_m}{K}\right) \qquad [4].$$

Predation and mimicry

All individuals (whatever their colour pattern) are attacked at the same baseline rate *p*, and have the same level of unpalatability *u* (i. e., they are equally defended). We assume that predation decreases as the number of individuals sharing the same colour pattern increases, as in previous models (Müller, 1879; Joron & Iwasa, 2005; Llaurens *et al.*, 2015).

We assume that the conspicuousness of the colour pattern has two opposite effects on predation risk. On the one hand, an increased conspicuousness increases the risk of being detected by predators, and therefore of being attacked (numerator terms in equations [5] – [8]). On the other hand, an increased conspicuousness makes the colour pattern easier to remember for predators (i. e., more salient), and therefore enhances protection brought by mimicry (Sherratt, 2002; Broom *et al.*, 2006) (in the denumerator terms in equations [5] – [8]). The translation of conspicuousness into salience is described by the translation term β_{wt} or β_m modelling the level of memorability induced in predators by a given level of conspicuousness. Individuals with wild-type and mutant colour pattern can then differ in their level of salience, β_{wt} x c_{wt} and β_m x c_m respectively (how the conspicuousness of their colour pattern triggers predator memorability and avoidance learning). The salience of the colour

pattern is therefore modelled as a function of the conspicuousness (c_{wt} or c_m) and the translation term (β_{wt} or β_m) assuming a positive linear relationship between conspicuousness and salience of the colour pattern. If $\beta_{wt} = 0$ or $\beta_m = 0$, the colour pattern is not salient even when it is conspicuous, and predator never associate the colour pattern with unpalatability (i. e., this is not a warning signal). We therefore focus on cases where $\beta_{wt} > 0$ and $\beta_m > 0$, i. e., when an increase in conspicuousness associates with an increase in salience (thereby triggering more rapid avoidance learning in predators and reducing predation).

We consider that our focal conspicuous defended species is not isolated but instead belongs to a mimicry ring, as often observed in nature (Mallet & Gilbert, 1995). To keep the model analytically tractable, we do not model explicitly the population dynamics of each species of the mimicry community. Instead we model the effects on the focal species of the local mimicry rings harbouring either the wild-type or the mutant colour pattern using fixed parameters M_{wt} and M_m respectively. Parameters M_{wt} and M_m capture the protection provided by the presence of all co-mimetic prey and therefore accounts for the abundance, the unpalatability, the conspicuousness and the salience associated with the mimicry ring (Tab. 1).

We consider that mutant individuals belong either to the same mimicry ring as wild-type individuals ('one mimicry ring hypothesis' hereafter), or to a distinct mimicry ring ('two mimicry ring hypothesis'):

One mimicry ring hypothesis. – We investigate the evolution of conspicuousness assuming that variations in conspicuousness are generalized by predators, so that individuals displaying the wild-type and the mutant colour pattern belong to the same mimicry ring (equations [5] and [6]). This one mimicry ring is characterized by the parameter M_{wt} (in the denominator terms in equations [5] and [6]). Wild-type and mutant colour pattern differ in their conspicuousness and, in most cases also in their salience $c_{wt} \times \beta_{wt} \neq c_m \times \beta_m$). Under the 'one mimicry ring

hypothesis', the changes in density of individuals displaying the wild-type and mutant colour pattern due to predation follow:

$$P_{wt} = \frac{-pc_{wt}N_{wt}}{1+u(\beta_{wt}c_{wt}N_{wt}+\beta_m c_m N_m)+M_{wt}} \qquad [5],$$

$$P_m = \frac{-pc_m N_m}{1+u(\beta_{wt}c_{wt}N_{wt}+\beta_m c_m N_m)+M_{wt}} \qquad [6].$$

Two mimicry ring hypothesis. – Alternatively, variations in conspicuousness may result in colour pattern perceived as different by predators. Therefore, we consider another scenario where wild-type and mutant colour pattern are not generalized by predators and may therefore match different mimicry rings characterized by parameters M_{wt} and M_m (equations [7] and [8]). In this scenario, wild-types and mutants have a distinct colour pattern with different associated salience. Wild-type and mutant colour patterns are thus perceived as distinct by predators. When $M_m = 0$, mutant individuals do not belong to any mimicry ring. Under the 'two mimicry ring hypothesis', the changes in density of individuals displaying the wild-type and mutant colour pattern due to predation follow:

$$P_{wt} = \frac{-pc_{wt}N_{wt}}{1+u\beta_{wt}c_{wt}N_{wt}+M_{wt}} \qquad [7],$$

$$P_m = \frac{-pc_m N_m}{1+u\beta_m c_m N_m+M_m} \qquad [8].$$

Final dynamical systems

To derive analytically the system of equations presented above, we rescale all variables to baseline growth rate and carrying capacity, as follows: $n_{wt} = \frac{N_{wt}}{K}$, rescaled density of wild-type individuals; $n_m = \frac{N_m}{K}$, rescaled density of mutant individuals; $\delta = \frac{p}{r}$, rescaled baseline mortality rate; $\tau = rt$ rescaled time unit; and $\lambda_{wt} = uK\beta_{wt}$ and $\lambda_m = uK\beta_m$ named rescaled deterrence factors. The dynamical system under the 'one mimicry ring hypothesis' becomes:

$$\begin{cases} \frac{dn_{wt}}{d\tau} = n_{wt}(1 - n_{wt} - n_m) - \frac{\delta c_{wt} n_{wt}}{1+(\lambda_{wt} c_{wt} n_{wt} + \lambda_m c_m n_m) + M_{wt}} \\ \frac{dn_m}{d\tau} = n_m(1 - n_{wt} - n_m) - \frac{\delta c_{wt} n_m}{1+(\lambda_{wt} c_{wt} n_{wt} + \lambda_m c_m n_m) + M_{wt}} \end{cases} \quad [9]$$

And under the 'two mimicry ring hypothesis':

$$\begin{cases} \frac{dn_{wt}}{d\tau} = n_{wt}(1 - n_{wt} - n_m) - \frac{\delta c_{wt} n_{wt}}{1+\lambda_{wt} c_{wt} n_{wt} + M_{wt}} \\ \frac{dn_m}{d\tau} = n_m(1 - n_{wt} - n_m) - \frac{\delta c_{wt} n_m}{1+\lambda_m c_m n_m + M_m} \end{cases} \quad [10]$$

We investigate analytically the evolution of conspicuousness by conducting invasion analyses on the systems of equations [9] and [10]. All analytical derivations are detailed in Supp. Information. We first derive the expression of the density n_{wt}^* at equilibrium when the population is composed solely of wild-type individuals (solution of $\frac{dn_{wt}}{d\tau} = 0$, assuming $n_m = 0$). We then determine the sign of the growth rate of the mutant population, assuming that mutants are rare within a population of wild-type individuals at equilibrium (sign of $\frac{dn_m}{d\tau}$, assuming $n_{wt} = n_{wt}^*$ and $n_m \ll n_{wt}$). If the sign of this growth rate is positive, then mutants can invade in the population. Given that invading mutants will eventually replace the wild type populations (as shown numerically in Supp. Fig. 1 and Supp Fig. 2), we can infer the equilibrium (fixation of the wild type or mutant colour pattern) from the invasion analysis.

RESULTS

1 – A decrease in conspicuousness is favoured within mimicry ring ('one mimicry ring hypothesis')

We explore the evolution of conspicuousness when wild-type and mutant colour patterns are perceived as similar by predators, and belong to the same mimicry ring. This is likely to apply when the mutant's conspicuousness only slightly differs from the wild-type's. The condition under which mutants can invade is when mutant conspicuousness is lower than that of the wild-type (analytical derivations detailed in Supp. Information):

$c_m < c_{wt}$ [11]

Under our model assumptions, selection therefore favours less conspicuous colour patterns within a single mimicry ring (Fig. 1). Such evolutionary process may occur via small-effect mutations modifying conspicuousness (with a completely cryptic colouration being the evolutionary stable strategy, as defined within the adaptive dynamics theoretical framework). The selective process underlying this evolution is straightforward: less conspicuous individuals are less detectable and simultaneously benefit from the protection provided by the mimicry ring.

2 – An increase in conspicuousness can be promoted by a switch in mimicry ring ('two mimicry ring hypothesis')

We then investigate the evolution of conspicuousness when the mutant colour pattern is perceived as distinct from the wild type colour pattern by predators, and eventually matches another mimicry ring. This is likely to apply when the mutant's conspicuousness strongly differs from the wild-type's (via a large-effect mutation). Importantly, one should not have the adaptive dynamics theoretical framework in mind because it would require to make the very unrealistic assumption that there is an infinite number of mimicry rings.

Our analytical results show that the level of conspicuousness under which mutants are advantaged when introduced in the wild-type population is:

$c_m < \hat{C}$ [12]

With $\hat{C}$ being the conspicuousness threshold value under which mutants are advantaged (analytical derivations detailed in Supp. Information). This threshold is expressed as:

$\hat{C} = c_{wt} \frac{1+M_m}{1+\lambda_{wt} c_{wt} n^*_{wt} + M_{wt}}$ [13]

The invasion of the mutant colour pattern thus crucially depends on the ratio:

$\left(1 + M_m\right) / \left(1 + \lambda_{wt} c_{wt} n^*_{wt} + M_{wt}\right)$ [14]

Effects of parameters on the invasion threshold $\hat{C}$ are summarized in Tab. 2 (associated analytical derivations are detailed in Supp. Information)

Contrary to results obtained under the 'one mimicry ring hypothesis', slightly less conspicuous mutants do not always invade, because of the costs associated with displaying a less protected alternative colour pattern (Fig. 2B-D). Overall, less conspicuous mutant colour patterns are frequently advantaged (Fig. 2B-D). For instance, a mutant with a non-conspicuous (cryptic) colour pattern ($c_m = 0$) always invades (because $\hat{C} > 0$), even when the mutant colour pattern does not match any mimicry ring.

Interestingly, mutants with a more conspicuous colour pattern than the wild type $(c_m > c_{wt})$ may be advantaged if the ratio [14] is superior to 1, i. e., if $M_m > \lambda_{wt} c_{wt}\, n^*_{wt} + M_{wt}$ (highlighted in red in Fig. 2D). Thus, for a more conspicuous mutant colour pattern to be positively selected, it requires that the alternative mimicry ring (M_m) provides better protection than the combination of the wild-type population $\left(\lambda_{wt} c_{wt}\, n^*_{wt}\right)$ and its mimicry ring (M_{wt}). By contrast, when the mimicry ring matching the wild-type colour pattern provides a great protection to wild-type individuals (high M_{wt}), this prevents mutant colour patterns from invading (Tab. 2).

The invasion of a more conspicuous mutant is then modulated by other parameters, such as the level of predation and unpalatability, as well as the salience of the wild type. Indeed, increased predation pressure (rescaled δ, Tab. 2) increases the range of conspicuousness values enabling the invasion of the mutant colour pattern: when the predation rate is high, a slight decrease in conspicuousness strongly favours the mutant, despite the cost associated with the switch to a less protected mimicry rings. By contrast, an increase either in the translation term in wild type colour pattern, i. e., the link between conspicuousness and salience (β_{wt}) or in the unpalatability (u) can prevent the invasion of mutant colour pattern (cf. effect of $\lambda_{wt} = uK\beta_{wt}$, Tab. 2). Indeed, those parameters both underlie the intensity of the number-dependent

selection driven by predator avoidance-learning (strength in number; λ_{wt}), increasing the protection incurred by the wild type population.

The salience associated with the mutant colour pattern (controlled by β_m; note however that parameter M_m also accounts for the salience in co-mimetic species) does not affect the invasion conditions of the mutant colour pattern. Indeed, we investigate the invasive conditions of the mutant colour pattern when N_m is small, so whatever the value of β_m, the term β_m x N_m, is also very small (in equations [5] – [8]). Therefore, only the salience associated with the wild-type phenotype (controlled by β_{wt}) matters. As noted above, the more salient and conspicuous the wild-type colour pattern is (high β_{wt}), the better it is protected, limiting the invasion of mutant colour patterns perceived as distinct by predators (Fig. 2). By contrast, if the salience associated with the wild-type colour pattern is low, i. e., when the wild-type colour pattern is not well learnt by predator, a more conspicuous mutant colour pattern can easily invade in the population (Fig. 2 and Supp. Fig. 3). Note that, in such case, the weak salience of the wild-type colour pattern is also integrated in the mimicry ring (M_{wt}) and can be compensated by an increased abundance or unpalatability of the co-mimetic species.

DISCUSSION

Evolution toward decreasing level of conspicuousness within mimicry ring

Our model predicts that mimetic colour pattern may evolve toward reduced conspicuousness and complete crypsis within mimicry rings (under the 'one mimicry ring hypothesis'). Less conspicuous individuals benefit from reduced detection by predators and therefore benefit from a lower predation rate than more conspicuous individuals. As long as the colour pattern is generalized by predators, all individuals within a mimicry ring benefit from the same reduction in predation risk, brought by the strength in number. Less conspicuous mutants act as selfish elements that may eventually replace the more conspicuous colour pattern, resulting

temporarily in an increased predation risk for all members of the mimicry ring, because predator learning would then be less efficient. Ultimately, this would lead to completely cryptic colour pattern that is no longer perceived as a warning signal by predators.

In natural communities of defended prey, mildly conspicuous colour patterns with a few salient features can indeed provide an effective aposematic signal. The defended butterflies from the Ithomiini tribe may be a relevant example of such aposematic patterns, because many Ithomiini species have transparent wings and mildly conspicuous colour patterns, resulting in a decrease in detectability by avian predators (Arias *et al.*, 2019). Under the 'one mimicry ring hypothesis', the evolution of complete crypsis is possible because we assume that mutant colour pattern is always recognized by predators as the same colour pattern as the wild-type one. In nature, however, actual variations of conspicuousness may result in colour pattern discriminations by predators (a feature that we do not account for in the one mimicry ring model), which should limit the decrease in conspicuousness within mimicry rings. Such colour pattern discrimination could explain the persistence of transparent cryptic wing pattern associated with some key salient features observed in Ithomiini clearwing species. Overall, selection pressure within mimicry rings may ultimately influence Müllerian mimetic interactions by favouring reduced detectability in some mimetic species, diminishing predation risk on less noticeable mimetic prey (Arias *et al.*, 2019).

Evolution of more conspicuous colour patterns can be promoted by mimicry switches

Our model highlights that a switch to more conspicuous colour pattern can be favoured when mutant colour pattern matches a better-protected mimicry ring (under the 'two mimicry ring hypothesis'). By considering the Müllerian mimetic environment in our model, we show that the conspicuousness of a colour pattern does not evolve independently from other aposematic species co-occurring in sympatry. Even if we assumed that conspicuousness does not associate

with a direct benefit (i. e., we considered a worst-case scenario; as highlighted under the 'one mimicry ring hypothesis' where complete crypsis is favoured), a switch to a distinct mimicry ring can still promote increased conspicuousness. This prediction is in line with a previous empirical finding. The colouration of the chemically-defended viceroy butterfly, *Limenitis archippus*, is thought to have evolved from a non-aposematic ancestral pattern to aposematic ones, mimicking *Danaus* species' colour patterns (Platt *et al.*, 1971; Prudic *et al.*, 2002; Mullen, 2006; Prudic & Oliver, 2008). The evolution of a more conspicuous pattern could thus stem from mimicry towards the well-defended Monarch butterflies living in sympatry.

Our study thus calls attention to the effect of ecological interactions with other defended species, and of the diversity of colour pattern in sympatric species on the evolution of aposematism in defended species.

Salience and its effect on memorability can contribute to the evolution of mimetic colour pattern

Traditionally, modelling studies investigating the evolution of aposematism do not consider mimetic interactions (Leimar *et al.*, 1986; Speed & Ruxton, 2005a, 2005b; Broom *et al.*, 2006), while those investigating the evolution and implications of mimicry generally consider all colour patterns to have the same impact on predator learning behaviour (Müller, 1879; Sherratt, 2006; Gompert *et al.*, 2011; Aubier *et al.*, 2017). One notable exception is the theoretical study by Franks *et al.*, (2009) where the authors show that aposematism may evolve in one defended species as a result of disengaging with undefended mimics. To our knowledge, our study corresponds to a first attempt to include conspicuousness and salience of warning signals, and mimetic interactions among defended species within the same theoretical framework. We precisely highlight that a mimicry switch can favour the invasion of a more conspicuous mutant when the wild-type colour pattern is poorly salient and not well learnt by predators.

The positive number-dependent protection gained by aposematic individuals can thus be modulated by the salience of the colour patterns, a feature that we included in our model. While our study focuses on the evolution of conspicuousness, variations in salience and its effect on predator memorability may have other important consequences for the evolution of colour patterns in mimetic communities. For instance, the high diversity of aposematic colour pattern observed within localities (Joron & Mallet, 1998; Briolat *et al.*, 2018) could be maintained by trade-offs between unpalatability, salience of the colour pattern and abundances in the different mimicry rings. In our study, we considered mimetic interactions without specifically modelling the abundance, the level of defences, and the salience of co-mimetic species. Nonetheless, our model constitutes a fundamental basis for such future theoretical research explicitly investigating the evolution of colour pattern in multiple co-mimetic species.

CONCLUSION

Overall, we highlight that the evolution of mimetic colour patterns in defended species depends on the abundance and salience of colour patterns. Our model shows that in a worst-case scenario, where conspicuousness does not bring any direct benefit (as immediate deterrence), the evolution of colour pattern with increased conspicuousness is possible when considering switches to distinct Müllerian mimicry rings. Considering mimetic community therefore opens a new angle to explain the evolution of the wide diversity of colour patterns: via number-dependent selection at the community level, more conspicuous colour pattern can be favoured. Further research taking into account mimetic interactions and variations in salience between warning signals are needed to better understand the evolution of aposematism.

DATA ACCESSIBILITY

The model is implemented in C++ and the code will be made available from a Dryad Digital Repository.

AUTHOR'S CONTRIBUTIONS

VL, TGA, ME and OS designed the study. OS and VL performed preliminary analyses not presented in the paper (simulations). TGA and LM wrote the mathematical model and solved it analytically. OS wrote the manuscript with contributions from all authors. All authors participated in constructive discussions and approved manuscript final version.

COMPETING INTERESTS

We declare no competing interests.

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REFERENCES

Arias, M., Mappes, J., Desbois, C., Gordon, S., McClure, M., Elias, M., Nokelainen, O., & Gomez, D. (2019) Transparency reduces predator detection in mimetic clearwing butterflies. *Functional Ecology*, **33**, 1110–1119.

Aronsson, M. & Gamberale-Stille, G. (2009) Importance of internal pattern contrast and contrast against the background in aposematic signals. *Behav Ecol*, **20**, 1356–1362.

Aubier, T.G., Elias, M., Llaurens, V., & Chazot, N. (2017) Mutualistic mimicry enhances species diversification through spatial segregation and extension of the ecological niche space. *Evolution*, **71**, 826–844.

Aubier, T.G. & Sherratt, T.N. (2015) Diversity in Müllerian mimicry: The optimal predator sampling strategy explains both local and regional polymorphism in prey. *Evolution*, **69**, 2831–2845.

Barnett, J.B., Scott-Samuel, N.E., & Cuthill, I.C. (2016) Aposematism: balancing salience and camouflage. *Biology Letters*, **12**, 20160335.

Briolat, E.S., Burdfield-Steel, E.R., Paul, S.C., Rönkä, K.H., Seymoure, B.M., Stankowich, T., & Stuckert, A.M.M. (2018) Diversity in warning coloration: selective paradox or the norm? *Biological Reviews*, **94**, 388–414.

Broom, M., Speed, M.P., & Ruxton, G.D. (2006) Evolutionarily stable defence and signalling of that defence. *Journal of Theoretical Biology*, **242**, 32–43.

Buechel, S.D., Boussard, A., Kotrschal, A., van der Bijl, W., & Kolm, N. (2018) Brain size affects performance in a reversal-learning test. *Proceedings of the Royal Society B: Biological Sciences*, **285**, 20172031.

Franks, D.W., Ruxton, G.D., & Sherratt, T.N. (2009) Warning signals evolve to disengage batesian mimics. *Evolution*, **63**, 256–267.

Gompert, Z., Willmott, K., & Elias, M. (2011) Heterogeneity in predator micro-habitat use and the maintenance of Müllerian mimetic diversity. *Journal of Theoretical Biology*, **281**, 39–46.

Greenwood, J.J.D., Cotton, P.A., & Wilson, D.M. (1989) Frequency-dependent selection on aposematic prey: some experiments. *Biological Journal of the Linnean Society*, **36**, 213–226.

Ham, A.D., Ihalainen, E., Lindström, L., & Mappes, J. (2006) Does colour matter? The importance of colour in avoidance learning, memorability and generalisation. *Behav Ecol Sociobiol*, **60**, 482–491.

Hill, G.E. (1996) Redness as a measure of the production cost of ornamental coloration. *Ethology Ecology & Evolution*, **8**, 157–175.

JORON, M. & IWASA, Y. (2005) The evolution of a Müllerian mimic in a spatially distributed community. *Journal of Theoretical Biology*, **237**, 87–103.

JORON, M. & MALLET, J. (1998) Diversity in mimicry: paradox or paradigm? *Trends in Ecology & Evolution*, **13**, 461–466.

LEIMAR, O., ENQUIST, M., & SILLEN-TULLBERG, B. (1986) Evolutionary Stability of Aposematic Coloration and Prey Unprofitability: A Theoretical Analysis. *The American Naturalist*, **128**, 469–490.

LINDSTEDT, C., EAGER, H., IHALAINEN, E., KAHILAINEN, A., STEVENS, M., & MAPPES, J. (2011) Direction and strength of selection by predators for the color of the aposematic wood tiger moth. *Behav Ecol*, **22**, 580–587.

LINDSTRÖM, L., ALATALO, R.V., LYYTINEN, A., & MAPPES, J. (2001) Predator experience on cryptic prey affects the survival of conspicuous aposematic prey. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 357–361.

LINDSTROM, L., ALATALO, R.V., LYYTINEN, A., & MAPPES, J. (2001) Strong antiapostatic selection against novel rare aposematic prey. *Proceedings of the National Academy of Sciences*, **98**, 9181–9184.

LLAURENS, V., JORON, M., & BILLIARD, S. (2015) Molecular mechanisms of dominance evolution in Müllerian mimicry. *Evolution*, **69**, 3097–3108.

MALLET, J. & GILBERT, L.E. (1995) Why are there so many mimicry rings? Correlations between habitat, behaviour and mimicry in Heliconius butterflies. *Biological Journal of the Linnean Society*, **55**, 159–180.

MARPLES, N.M. & KELLY, D.J. (1999) Neophobia and Dietary Conservatism:Two Distinct Processes? *Evolutionary Ecology*, **13**, 641–653.

MARPLES, N.M., KELLY, D.J., THOMAS, R.J., & HARRISON, R. (2005) Perspective: the evolution of warning coloration is not paradoxical. *Evolution*, **59**, 933–940.

MCCLURE, M., CLERC, C., DESBOIS, C., MEICHANETZOGLOU, A., CAU, M., BASTIN-HÉLINE, L., BACIGALUPO, J., HOUSSIN, C., PINNA, C., NAY, B., LLAURENS, V., BERTHIER, S., ANDRAUD, C., GOMEZ, D., & ELIAS, M. (2019) Why has transparency evolved in aposematic butterflies? Insights from the largest radiation of aposematic butterflies, the Ithomiini. *Proceedings of the Royal Society B: Biological Sciences*, **286**, 20182769.

MCGRAW, K.J., HILL, G.E., & PARKER, R.S. (2005) The physiological costs of being colourful: nutritional control of carotenoid utilization in the American goldfinch, Carduelis tristis. *Animal Behaviour*, **69**, 653–660.

MULLEN, S.P. (2006) Wing pattern evolution and the origins of mimicry among North American admiral butterflies (Nymphalidae: Limenitis). *Molecular Phylogenetics and Evolution*, **39**, 747–758.

MÜLLER, F. (1879) Ituna and Thyridia; a remarkable case of mimicry in butterflies (transl. by Ralph Meldola from the original German article in Kosmos, May 1879, 100). *Transactions of the Entomological Society of London*, 20–29.

PLATT, A.P., COPPINGER, R.P., & BROWER, L.P. (1971) Demonstration of the Selective Advantage of Mimetic Limenitis Butterflies Presented to Caged Avian Predators. *Evolution*, **25**, 692–701.

PRUDIC, K.L. & OLIVER, J.C. (2008) Once a Batesian mimic, not always a Batesian mimic: mimic reverts back to ancestral phenotype when the model is absent. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1125–1132.

PRUDIC, K.L., SHAPIRO, A.M., & CLAYTON, N.S. (2002) Evaluating a putative mimetic relationship between two butterflies, Adelpha bredowii and Limenitis lorquini. *Ecological Entomology*, **27**, 68–75.

ROPER, T.J. & REDSTON, S. (1987) Conspicuousness of distasteful prey affects the strength and durability of one-trial avoidance learning. *Animal Behaviour*, **35**, 739–747.

RUXTON, G.D. (2019) Defensive Coloration. *Encyclopedia of Animal Behavior (Second Edition)* (Choe, J.C. ed). Oxford: Academic Press, pp. 298–303.

SHERRATT, T.N. (2002) The coevolution of warning signals. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **269**, 741–746.

SHERRATT, T.N. (2006) Spatial mosaic formation through frequency-dependent selection in Müllerian mimicry complexes. *Journal of Theoretical Biology*, **240**, 165–174.

SIDDALL, E.C. & MARPLES, N.M. (2008) Better to be bimodal: the interaction of color and odor on learning and memory. *Behav Ecol*, **19**, 425–432.

SILLÉN-TULLBERG, B. (1985) Higher survival of an aposematic than of a cryptic form of a distasteful bug. *Oecologia*, **67**, 411–415.

SPEED, M.P. & RUXTON, G.D. (2005a) Warning Displays in Spiny Animals: One (more) Evolutionary Route to Aposematism. *Evolution*, **59**, 2499–2508.

SPEED, M.P. & RUXTON, G.D. (2005b) Aposematism: what should our starting point be? *Proceedings of the Royal Society B: Biological Sciences*, **272**, 431–438.

VALKONEN, J., NISKANEN, M., BJÖRKLUND, M., & MAPPES, J. (2011) Disruption or aposematism? Significance of dorsal zigzag pattern of European vipers. *Evol Ecol*, **25**, 1047–1063.

WÜSTER, W., ALLUM, C.S.E., BJARGARDÓTTIR, I.B., BAILEY, K.L., DAWSON, K.J., GUENIOUI, J., LEWIS, J., MCGURK, J., MOORE, A.G., NISKANEN, M., & POLLARD, C.P. (2004) Do aposematism and Batesian mimicry require bright colours? A test, using European viper markings. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 2495–2499.

FIGURES

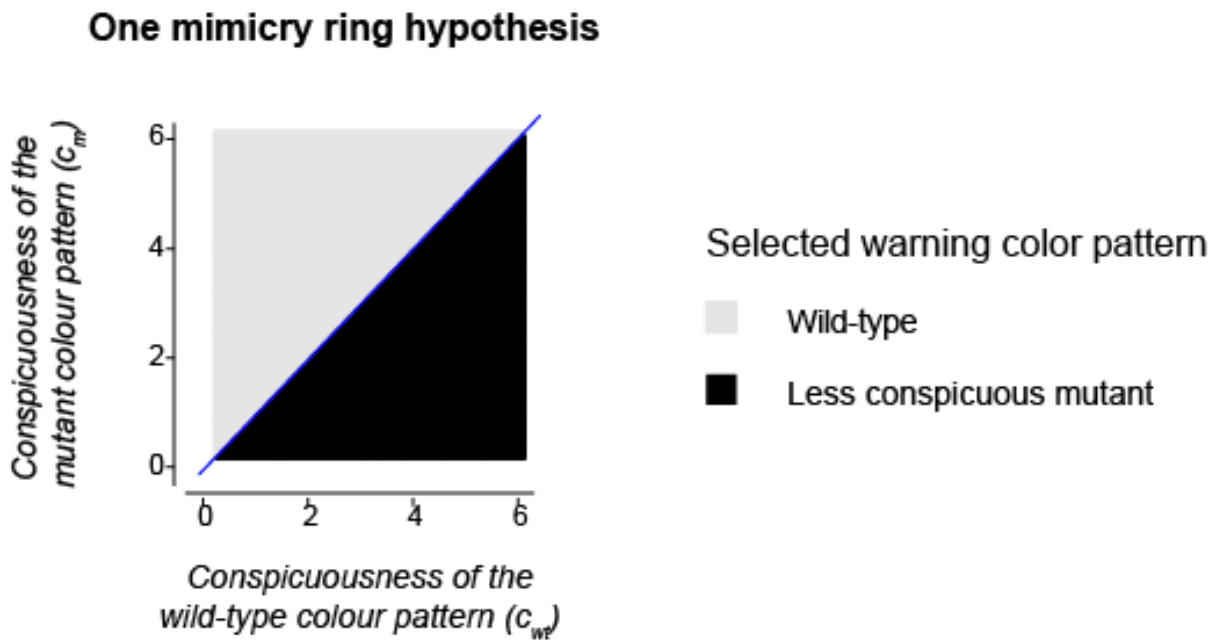

Figure 1: Evolution of conspicuousness under the 'one mimicry ring hypothesis' where wild-type and mutant colour patterns are perceived by predators as similar.

Inference of the evolutionary equilibrium from the invasion analysis, with wild-type and mutant individuals having different levels of conspicuousness (c_{wt}, c_m). The diagonal blue line represents cases where $c_{wt} = c_m$. Colour scale indicates the sign of the derivative $\frac{dN_m}{dt}$ after introduction of the mutant (derived analytically; see Supp. Information). Light grey represents cases where $\frac{dN_m}{dt} \leq 0$ (so the mutant does not invade) and black represents cases where $\frac{dN_m}{dt} > 0$ (so the mutant invades, ultimately leading to the fixation of the mutant colour pattern; as shown in Supp. Fig. 1). We get the same invasion condition whatever the parameters implemented.

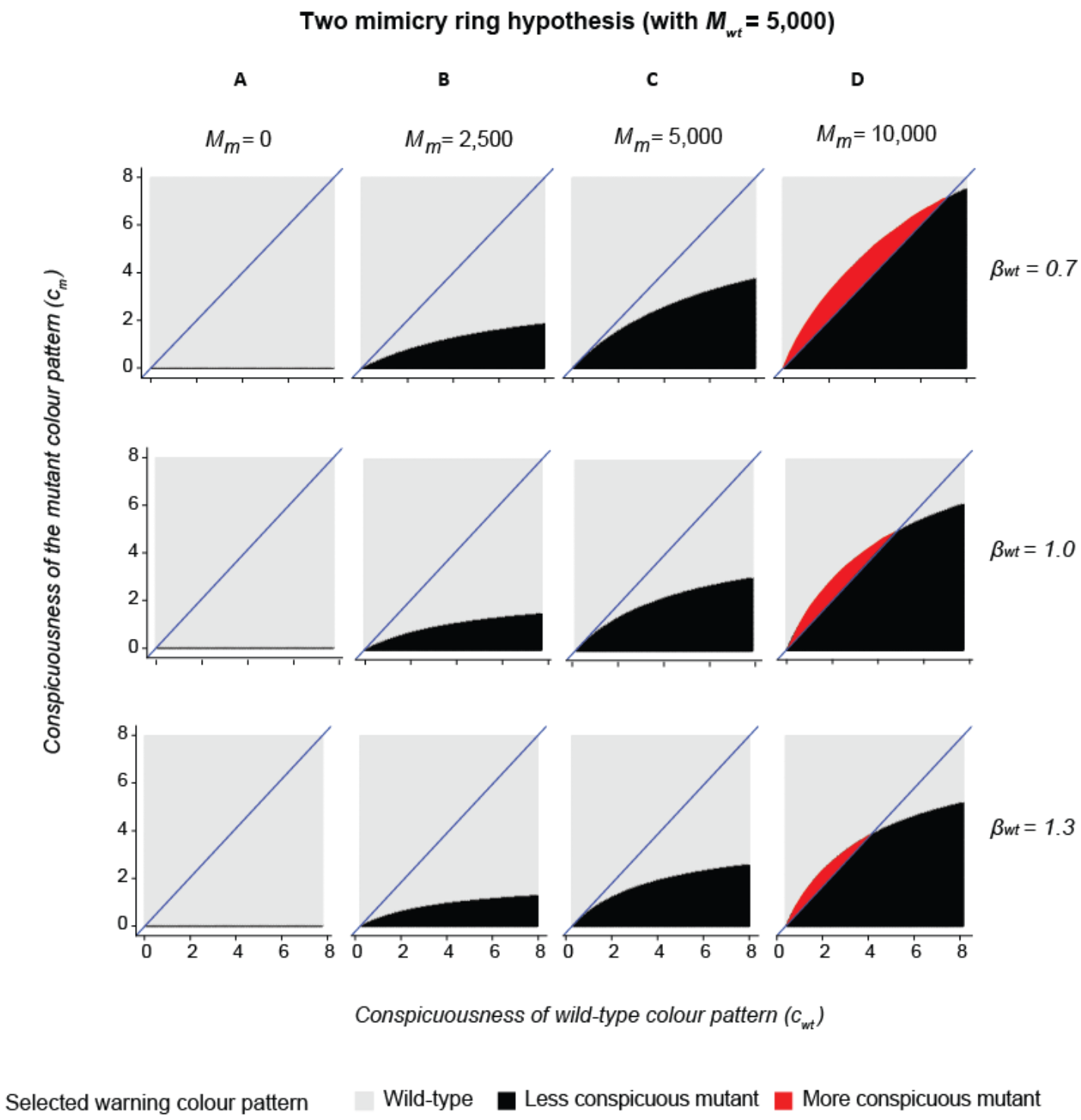

Figure 2: Evolution of conspicuousness under the 'two mimicry ring hypothesis'; wild-type and mutant colour patterns are perceived by predators as different, and mutants may belong to a distinct mimicry ring.

Inference of the evolutionary equilibrium from the invasion analysis, with wild-type and mutant individuals having different levels of conspicuousness (c_{wt}, c_m). The diagonal blue line

represents cases where $c_{wt} = c_m$. Colour scale indicates the sign of the derivative $\frac{dN_m}{dt}$ after introduction of the mutant (derived analytically; see Supp. Information). Light grey represents cases where $\frac{dN_m}{dt} \leq 0$ (so the mutant does not invade) and black represents cases where $\frac{dN_m}{dt} > 0$ (so the mutant invades, ultimately leading to the fixation of the mutant colour pattern; as shown in Supp. Fig. 2).

The mutant colour pattern may be unique within the mimetic community ($M_{wt} = 5{,}000; M_m = 0$) (A). Alternatively, the mutant colour pattern may associate with a mimicry switch with the mimicry ring matching the mutant colour pattern being half less protective ($M_{wt} = 5{,}000; M_m = 2{,}500$) (B), equally-protective ($M_{wt} = 5{,}000; M_m = 5{,}000$) (C) or more protective ($M_{wt} = 5{,}000; M_m = 10{,}000$) (D) than the mimicry ring matching the wild-type colour pattern .

We considered different wild-type salience β_{wt} (remember that β_m has no effect on the invasion pattern) with from top to bottom: $\beta_{wt} = 0.7$, $\beta_{wt} = 1$ and $\beta_{wt} = 1.3$. Other parameter values before rescaling the system of equations are: p = 0.5; u = 1; K = 1,000; r = 2.

TABLE

Parameter	Description
$N_{wt}(t)$, $N_m(t)$	Number of individuals displaying the wild-type or mutant colour pattern at time t
c_{wt}, c_m	Conspicuousness of the wild-type or mutant colour pattern
M_{wt}	Reduction of the predation risk due to the mimicry ring matching the wild-type colour pattern (includes the abundance, unpalatability, the conspicuousness and the salience)
M_m	Reduction of the predation risk due to the mimicry ring matching the mutant colour pattern (includes the abundance, unpalatability, the conspicuousness and the salience)
β_{wt}, β_m	Translation term modulating the effect of conspicuousness on salience in the wild-type or mutant colour pattern
u	Unpalatability
p	Baseline predation rate
r	Baseline growth rate
K	Carrying capacity

Table 1. Notations before rescaling the system of equations

Parameter	**Sensitivity of the invasion condition**	**Meaning**
M_{wt}, the *wild-type* mimicry ring	$\frac{\partial \hat{C}}{\partial M_{wt}} < 0$	Higher protection provided by the mimicry ring matching the wild-type colour pattern (M_{wt}) **decreases** the range of conspicuousness values enabling the invasion of the mutant.
M_m, the *mutant* mimicry ring	$\frac{\partial \hat{C}}{\partial M_m} > 0$	Higher protection provided by the mimicry ring matching the mutant colour pattern (M_m) **increases** the range of conspicuousness values enabling the invasion of the mutant.
λ_{wt} rescaled deterrence factor (with $\lambda_{wt} = uK\beta_{wt}$)	$\frac{\partial \hat{C}}{\partial \lambda_{wt}} < 0$	Higher deterrence factor λ **decreases** the range of conspicuousness values enabling the invasion of the mutant.

δ, rescaled baseline mortality rate	$\frac{\partial \hat{C}}{\partial \delta} > 0$	Increased baseline predation pressure (δ) **increases** the range of conspicuousness values enabling the invasion of the mutant.
c_{wt}, conspicuousness of the wild-type colour pattern	$\frac{\partial \hat{C}}{\partial c_{wt}} > 0$	Higher conspicuousness of the wild-type colour pattern (c_{wt}) **increases** the range of conspicuousness values enabling the invasion of the mutant.

Table 2. Sensitivity to parameters of the invasion conditions, assuming the 'two mimicry ring hypothesis'. The mutant colour pattern can invade when its conspicuousness c_m is inferior to the threshold conspicuousness $\hat{C}$.