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Effect of variation in defensive mechanisms of mimics: quasi-Batesian mimicry

Vliv variability v obranných mechanismech mimetiků na chování predátorů: quasi-Batesovské mimikry

Bachelor’s thesis

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Statement

I declare that I have prepared the thesis independently and that I have listed all the information sources and literature used. Neither this thesis nor any substantial part of it has been submitted for another or the same academic degree.

Prague, 25. 4. 2025 Johana Vinšová

Student's signature

Outline

1 Abstract

There are various types of defence mechanisms used by prey to escape detection by predators. However, many species use warning signals to inform predators about their unpalatability or toxicity. Some prey species closely resemble each other by sharing warning signals and gain protection from predators. This adaptation is defined as "mimicry.” According to the type of defence, we distinguish between Müllerian and Batesian mimicry. Müllerian mimicry consists of mutual relationship, where two or more equally unpalatable or toxic species (co-mimics) resemble each other. Batesian mimicry is defined as protection based on imitation of unpalatable species (the model) by another species (the mimic), where the mimic lacks any form of chemical or mechanical defence. In contrast, quasi-Batesian mimics possess certain level of defence (for example, partial unpalatability or unpleasant taste) resembling another, better protected species (the model). Unlike Batesian mimicry, where the mimic is completely undefended, the quasi-Batesian mimic has its own defence mechanisms, although they are less intense than those of a model. Depending on the level of defence and frequency, quasi-Batesian mimic can positively or negatively affect survival rate or fitness of model species.

Key words: mimicry, defence, quasi-Batesian, Batesian, Müllerian, aposematism, warning signals

Abstrakt

Existuje řada obranných mechanismů, které kořist využívá k úniku před predátory. Mnohé druhy používají výstražné signály, kterými predátory informují o své nepoživatelnosti nebo toxicitě. Některé organismy se navzájem podobají sdílením těchto výstražných signálů, díky čemuž získávají výhodu při ochraně před predátory. Tato adaptace je definována jako „miméze.“ Podle způsobu obrany obecně rozlišujeme Müllerovskou a Batesovskou mimézi. Müllerovská miméze spočívá ve vzájemném napodobení dvou nebo více stejně nejedlých či toxických druhů (ko-mimetici). Batesovská miméze je definována jako způsob obrany založený na napodobování nepoživatelného druhu (model) jiným (mimetik), přičemž mimetik postrádá jakoukoli formu chemické nebo mechanické obrany. Oproti tomu, quasi-Batesovská miméze spočívá v tom, že se druh (mimetik) s určitou úrovní obrany (například částečná nepoživatelnost nebo nepříjemná chuť) podobá jinému, lépe chráněnému druhu (model). Na rozdíl od Batesovské miméze, kde mimetik zcela postrádá vlastní obranu, má quasi-Batesovský mimetik své vlastní obranné mechanismy, přestože jsou méně účinné než u modelového druhu. V závislosti na stupni obrany a četnosti výskytu může quasi-Batesovský mimetik pozitivně nebo negativně ovlivňovat přežívání či fitness modelového druhu.

Klíčová slova: miméze, obrana, quasi-Batesovské, Batesovské, Müllerovské, aposematismus, varovné signály

2 Introduction

The ability to avoid predators based on mimicry varies across animal kingdom. It has been widely observed in both vertebrates and invertebrates, terrestrial, fresh water, even marine species included and there are multiple kinds of strategies so far recorded (Ruxton et al., 2004). Mimicry can be visual, behavioural, vocal or else (Ruxton et al., 2004). Mimicry is possessed by two or more species sharing a warning signal which we refer to as aposematism. Aposematism is described as a presence of effective anti-predator defence, chemical or mechanical, which is signalled to potential predators typically by visuals, such as high-contrast or vividly saturated coloration, but may also include acoustic or chemical modalities, functioning to enhance predator learning and avoidance. The difference between Batesian and Müllerian mimicry depends on the fact that, Müllerian co-mimics tend to be toxic or strongly unpalatable, while Batesian mimics imitate models but are palatable (Turner, 1987). While Batesian and Müllerian mimicry definition is binary, quasi-Batesian mimicry describes relationships where the mimic is less defended than model, but not completely palatable. Therefore, the cost or benefit to the model depends on the mimic's level of defence and other factors. As a result of that, quasi-Batesian mimicry is perceived more as a continuum. However, predator-prey interactions are influenced by many other factors, such as prey distastefulness, presence of alternative prey, predator learning and generalisation or predator level of hunger. For example, Barnett et al. (2007) demonstrated that avian predators had higher number of attack attempts on distasteful prey when food restricted (Barnett et al., 2007). In this work, I am summarizing current knowledge with particular emphasis on the effect of variation in defensive mechanisms of quasi-Batesian mimicry, focusing on antipredator strategies and predator responses, which critically shape the evolutionary dynamics of mimicry systems.

3 Theory

3.1 Concepts of Mimicry

Despite multiple observations throughout history, focused on conspicuous similarities between different organisms, the first scientist who briefly summarized the resemblance of one species to another, was Henry W. Bates. Fascinated by the study of Amazonian butterflies, he communicated the matter in letters with Ch. Darwin and J. S. Henslow (Ruxton et al., 2004). He noted that edible butterfly species such as *Leptalis* (now included within *Pieridae*) bore a strong resemblance to unpalatable *Heliconid* butterflies such as *Heliconius erato* and *Heliconius melpomene* in the Amazon in order to escape predators (Bates, 1862). Thus, this is what differs Batesian mimicry from Müllerian mimicry interaction, where it is assumed that two toxic or distasteful species are mimicking each other (Müller, 1878). As a result of that, Müllerian mimicry relationship is considered mutualistic, while Batesian mimicry is referred to as parasitic (Speed et al., 1999). By pointing out this phenomenon, Bates was able to answer a question of Alfred R. Wallace, whose letter to Darwin during 1860 contained a confusion he personally described as *"The repetition of the forms and colours of animals in distinct groups, but the two always occurring in the same country and generally on the very same spot."* Later, Darwin included the observations of Bates in the fourth edition of "The Origin of Species" (Sherratt, 2008). Bates' classic hypothesis predicted Batesian mimics as palatable and undefended while resembling unpalatable model (Bates, 1862). Turner (1970) used empirical study of Clarke and Sheppard (1962) to form ecological theory demonstrating the role of frequency-dependent selection impact on mimicry in *Papilio dardanus*, showing how female-limited polymorphic forms mimic various local unpalatable butterflies such as *Planema poggei*. He emphasized that success of Batesian mimics varies with predator pressure and model abundance.

Talking about Müllerian mimicry, the two unpalatable species resembling each other (referred to as "co-mimics"), this occurrence in butterflies was at first observed by naturalist Johannes F. Müller in Brazil (Sherratt, 2008). He also communicated the matter with Darwin through letters and later published the theory, assuming this type of mimicry worked as a kind of protection against predation risk too (Müller, 1878). However, this statement raised many questions and to both Bates and Wallace, the hypothesis seemed a lot unclear. For example, Wallace (1882) suggested that to a predator, only one of the documented species might appear as unpalatable even though both defend themselves, pointing out the case might be more Batesian.

Skelhorn and Rowe (2006) provided empirical evidence strongly supporting the hypothesis of equally defended Müllerian mimics as one of the surviving strategies based on testing naive predator learning with domestic chicks and unpalatable crumbs soaked in quinine and Bitrex (see chapter 4.1.1 for more detail). All this concludes that mimicry theory has progressed from fixed definitions to dynamic, context-dependent models, the field now recognizes mimicry as a fluid continuum governed by multisensory signals, ecological context, and predator experience.

Later on, it was Speed (1993) who introduced the term "quasi-Batesian mimicry" in order to describe model-mimic systems where both species are defended but unequally, which he originally deducted from work of Turner et al. (1984) introducing theoretical Monte Carlo model, and Huheey (1961), who pointed out that edibility is perceived as a scale. Speed's (1993) work expanded mimicry theory by proposing that mimicry exists on a continuum from Batesian to Müllerian, rather than separate categories. The term of "protective deceptive mimicry" is now commonly used when relating to the quasi-Batesian protection, strongly supporting the theory of parasitic relationship between mimic and a model. Looking onto this issue from a different angle, quasi-Batesian models can have a protective impact over their rare mimics. According to Pfennig et al. (2001) mimics are more frequently attacked with a model absent.

3.2 Theoretical Models of Mimetic Relationships

Speed (1993) presented a theoretical work based on the study of Turner et al., (1984) who introduced the Monte Carlo computer simulation program, reframing the existing dichotomy of Batesian and Müllerian mimicry. Speed proposed a continuum model, where the relationship between mimic and model was influenced by relative levels of defence and the frequency of encounters with predators. The concept of quasi-Batesian mimicry was introduced to describe systems where mimics are partially defended and may either benefit from or degrade the warning signal of better defended models. According to Turner, the fitness of mimics is density-dependent: positively for Müllerian mimics (more protection when common) and negatively for Batesian mimics (more protection when rare). The computer model thus gives results which conform with some of the traditionally accepted differences between Batesian and Müllerian mimicry (Turner et al., 1984). Based on the mathematical model, Turner et al. suggested that unpalatable mimics bring benefit to both themselves and their models as they become more common, while palatable mimics increase predation risk for the model, validating classical distinctions between Müllerian and Batesian mimicry. To add, they proposed a third class, “neutral mimicry,” describing rare or marginally palatable species that do not significantly affect model survival.

Speed (1993) elaborated the concept using a similar computer system he referred to as “Pavlovian Predator” involving a model of stimulus conditioning and learning and forgetting algorithm. The difference between models was made in contrast of hunger levels as Turner used stochastic model where the hunger level is constant without any impacts (Turner et al., 1984) but Speed described a model where predator is assumed to find sufficient alternative prey to actually reach constant hunger level (Speed, 1993). According to Speed’s predictions, learning is influenced by two key factors: the rate of learning depending on the intensity of prey palatability and the asymptotic attack probability representing the predator's eventual likelihood of attacking prey species based on its palatability. Extremely palatable or unpalatable prey leads to rapid learning, while neutral prey results in slower learning. Over time, forgetting occurs, causing attack probabilities to return to the naive level through a decelerating process. This dynamic system allows the predator's behaviour to adapt based on learning and forgetting, providing insights into how predator decision-making influences mimicry dynamics. Both Speed (1993) and Turner et al. (1984) proposed jacamars, insectivorous avian predators, as the theoretical naive predators involved in their studies. Results presented concluded similar as in Turner’s (1984) work that Müllerian co-mimics always benefit from equal spectrum of unpalatability when common while mimics less defended than their models (therefore considered quasi-Batesian mimics) decrease the protection of the model. To add, Speed's (1993) findings also suggested that neutrally palatable and some unpalatable (quasi-Batesian) mimics can also have negative impact on their models, being more Batesian-like, which also depends on prey density. However, Speed (1993) also pointed out that extinction effects, where repeated exposure to neutral or mildly unpleasant prey weakens previously learned aversions, further explain how predator behaviour can revert to a naive state. These insights highlight the behavioural flexibility of predators and demonstrate how attack probabilities are influenced by prey palatability spectrum, rather than following rigid rules. Compared to earlier models, such as that of Turner et al. (1984), which lacked the capacity to simulate such behavioural plasticity, the Pavlovian predator model offers a more general and realistic framework. Overall, this synthesis of psychological theory and ecological modelling challenges traditional mimicry theory and highlights the importance of learning and perception in predator-prey interactions. Classic hypothesis was also supported based on higher rate of predation of models when mimic density increases even when unpalatable mimics (considered quasi-Batesian mimics) are present in higher numbers.

Speed and Turner (1999) then continued exploring mimicry variability across a spectrum of defence intensity. They described continuum which divides edible prey from those possessing effective defences such as toxicity or other harmful effects. Using Rescorla-Wagner (1972) and Bush-Mosteller (1955) modelling (also including learning and forgetting), to explain how different predator strategies would impact the evolutionary stability of mimicry systems, where prey is defended to varying degrees. In their work, they supported the idea that moderately defended mimics may sometimes function as Batesian and other times as Müllerian, depending on ecological context. They also pointed out that warning signal polymorphism in mimetic species often correlates with palatability and may extend into defended species via quasi-Batesian mechanisms. They concluded that classical mimicry theory, which divides interactions into separate categories of Batesian and Müllerian mimicry, failed to account for variation in predator learning and memory (Speed and Turner, 1999).

Speed (2001) put more emphasis on mimetic polymorphism. He proposed that some of the most striking cases of polymorphism occur in species traditionally considered chemically defended, challenging the classical view that polymorphism is confined to edible, Batesian mimics. It was previously confirmed that colour and pattern vary among aposematic species (Speed, 2001). Based on empirical evidence, he suggested possible impacts of prey availability on predator interactions, as prey population density plays crucial role in shaping the dynamics of mimicry. While the traditional view holds that increasing mimic density is harmful to mimics, the author argues that under certain conditions, particularly when predator satiation occurs, Batesian mimics may actually benefit from higher densities. Additionally, the idea that prey species vary in their edibility, with some being more or less attractive to predators, introduces further complexity to the dynamics of mimicry (Speed, 2001). This shift from traditional assumptions provides new insights into how mimicry systems evolve, particularly in the context of Batesian and Müllerian mimicry. Furthermore, polymorphism plays a significant role in this process. As predator preferences shift and densities of mimics and models fluctuate, polymorphic mimetic populations may emerge, with different mimics occupying varying niches within the predator-prey dynamic (Speed., 2001.) This polymorphism can further enhance the stability of mimicry complexes by providing a diversity of mimic types, which can help prevent predators from focusing their avoidance behaviour on a single mimic form. Thus, polymorphism is an important evolutionary factor in the persistence and effectiveness of mimicry systems, contributing to their resilience and adaptability in fluctuating ecological conditions (Speed, 2001).

Balogh et al. (2008) followed up the work of Turner and Speed (1999) by testing how variation in chemical defences influences predator learning along the mimicry spectrum by also implementing a modified Rescorla-Wagner associative learning model of classical conditioning to simulate the behaviour of virtual predators. Prey was represented by visual signals associated with either fixed or variable levels of unpalatability. The model simulated prey types corresponding to uniform toxin profiles and others with mixtures, mimicking a spectrum from quasi-Batesian to quasi-Müllerian and super-Müllerian mimicry. Quasi-Müllerian mimicry occurs when a mimic with weaker or no defences still contributes to predator learning and benefits the model, while Super-Müllerian mimicry describes a scenario where a less defended mimic is more beneficial to the model species than an equally defended mimic (Balogh et al, 2008). Virtual predators were exposed to repeated “encounters” with prey signals across simulated learning trials. The scenarios varied in the strength and diversity of chemical defences, as well as the number of learning sessions, to explore the influence of toxin heterogeneity on associative learning. Each simulation tracked how quickly a predator learned to associate prey signals with unpalatability and reduced its attack rates accordingly. Balogh et al. (2008) also incorporated an impact of surprise in trials, which increases associability. Results showed that variation in toxin type or intensity significantly accelerated learning in the model predators. This suggests that diversity in chemical defence enhances signal memorability, therefore increasing protection for all prey sharing warning signal. The findings provide theoretical support for expanding mimicry classifications to include quasi-Müllerian relationships (Balogh et al., 2008).

The overall work by Turner (1984), Speed (1993), and Balogh et al. (2008) reshaped our understanding of mimicry by emphasizing a dynamic continuum rather than a discrete Batesian-Müllerian dichotomy. Speed's (1993) Pavlovian predator model introduced predator learning, forgetting and hunger level as key factors in mimicry dynamics, pointing to quasi-Batesian outcome. Speed (1993) also highlighted polymorphism as an adaptive response to fluctuating predation pressures, even in defended species. Balogh et al. (2008) confirmed that chemical variability accelerates predator learning, enhancing signal effectiveness. They expanded the theory about mimicry being perceived as a continuum by demonstrating how toxin diversity accelerates predator learning and enhances signal memorability, incorporating the phenomenon of possible quasi-Müllerian and super-Müllerian mimicry in mimicry classifications (Balogh et al., 2008).

3.3 The Role of Aposematism

Let's start with general questions. What exactly is aposematism and how do we define it? For a brief comparison, there are organisms carrying crypsis patterns to escape danger, therefore they avoid predators by matching the background or imitate an inanimate object, commonly known as "masquerade," also considered as a type of protective mimicry (Ruxton et al., 2004). This means crypsis and masquerade are the exact opposites of aposematism, where an individual presents conspicuous warning signals to inform the predator directly that they are not a good option to choose (Ruxton et al., 2004). An aposematic individual is usually having conspicuous colour pattern or body markings, even though aposematic signals are not just visual, animals use other kinds of communication too, such as behavioural, chemical or vocal. These warning signals typically indicate that the prey is toxic, distasteful, or dangerous in some way, and function as an honest advertisement of chemical or physical defence mechanisms (Ruxton et al., 2004). It could be a good strategy, if we leave out predator learning – there will always be aposematic individuals making a sacrifice to naive predators yet unfamiliar with the warning message, or different species evolving similar appearance, which might or might not be beneficial, depending on the palatability continuum between Batesian and Müllerian mimicry. In Müllerian mimicry, aposematism evolves through mutual reinforcement: multiple unpalatable or toxic species, such as *Heliconius erato* and *Heliconius melpomene* butterflies, converging on a common warning signal that predators learn to avoid more rapidly due to increased exposure (Müller, 1878). To Müllerian mimics, chemical defence is crucial as it makes predators avoid them based on their level of toxicity or unpalatability, moreover, the coloration is often based on high colour contrasts against the dark background such as bright red, orange or yellow against the dark or green background (Rowe & Guilford, 1999). In the contrary, Batesian mimicry involves the exploitation of aposematic signals by palatable species that are less defended or not defended at all. For example, *Papilio dardanus* female morphs mimic unpalatable models like *Amauris niavius* and *Danaus chrysippus* to deceive predators (Turner, 1970). While mimics benefit from this deception, their presence can potentially degrade the efficacy of the warning signal if they become too common, causing predators to resume sampling prey with the once-reliable aposematic pattern (Speed, 1993). Species such as the monarch butterfly (*Danaus plexippus*) and its mimic, the viceroy butterfly (*Limenitis archippus*), have long served as models for exploring the boundaries between aposematism, mimicry and signalling. Initially considered a classic Batesian system, later studies revealed that the viceroy may possess its own chemical defences, inserting it on the spectrum between Batesian and Müllerian mimicry (Ritland & Brower, 1991).

In summary, aposematism serves as the informational basis of mimicry systems, providing the template upon which both mutualistic (Müllerian) and deceptive (Batesian) mimicry are constructed.

4 Empirical Evidence

4.1 Predator Responses

Empirical investigations into mimicry systems have provided critical insight into how predators, particularly birds, respond to aposematic and mimetic prey. Avian predators are ideal subjects for mimicry research due to their advanced colour vision, capacity for associative learning and flexible foraging strategies. Moreover, it is possible to observe predator-prey interactions in both field and laboratory experiments.

4.1.1 Predator Learning and Dynamics of Unequally Defended Prey

An empirical evidence focused on quasi-Batesian continuum was made by Speed (1990) as he investigated how domestic chickens (*Gallus gallus domesticus*) learn to avoid moderately unpalatable prey and whether they continue to attack such prey after learning. In the experiment, broiler chickens were trained to drink from a container with blue coloured water, which was palatable. In addition, they were presented with green coloured water containing solution of quinine dihydrochloride, making it distasteful. Over successive trials, the percentage of birds accepting the quinine laced water decreased but stabilized at approximately 36%, indicating that the birds did not completely avoid the unpalatable stimulus (Speed, 1990 as cited in Speed, 1999). This behaviour suggests that predators may balance the potential benefits against the aversive taste, rather than entirely avoiding moderately unpalatable prey (see chapter 4.1.4. Trade-offs Between Nutritional State and Toxic Load for more). Such findings challenge the assumption that all defended prey is completely avoided by predators and support the concept of quasi-Batesian mimicry, where mildly defended species may not possess protection but dilute it (Speed, 1999).

Another experiment with domestic chicks was made by Skelhorn and Rowe (2005), as they investigated whether avian predators could learn to avoid unpalatable prey more effectively when the prey types are chemically distinct. Artificial prey consisted of red coloured crumbs sprayed with either quinine sulphate solution, Bitrex solution or a 1:1 cocktail mixture of both chemicals. Each group received 20 red crumbs: one group received only quinine-flavoured, another Better-favoured, and the third a mix of both. A control, palatable green crumb group was also used. Crumbs were placed one at a time in an arena marked with a grid to control for position. Chicks underwent seven training trials, with each trial ending after 16 crumbs were attacked or after a fixed time. The researchers recorded the number of red crumbs attacked and latency to switch from green to red prey. Results showed that chicks exposed to both chemical types learned to avoid red crumbs faster and retained the avoidance better than those exposed to only one chemical. This suggests that chemical diversity among Müllerian mimics enhances predator learning and memory (Skelhorn & Rowe, 2005).

Following up with next experiment, Skelhorn and Rowe (2006) tested whether visually distinct mimetic prey offer greater protection when their colour patterns are associated with different chemical defences. Domestic chicks were used as predators. Artificial prey was made by spraying crumbs with either quinine sulphate solution or a Bitrex solution. The crumbs were then dyed either red or black using food colouring. Chicks were assigned to experimental groups: two groups received red and black crumbs flavoured with the same chemical (either both quinine or both Bitrex), and two groups received red and black crumbs with different chemicals (one colour Bitrex, the other quinine). Each chick was allowed to attack 16 crumbs placed individually in an experimental arena. All groups successfully learned to avoid unpalatable prey. However, in contrast to previous findings using visually identical prey, no significant difference in avoidance learning speed or memory retention was observed between groups exposed to chemically distinct versus chemically identical prey. These results indicate that chemical diversity does not enhance predator learning when visual cues differ, suggesting that visual signal distinction alone may be sufficient for avoidance learning in some mimetic systems (Skelhorn & Rowe, 2006).

Next research supporting Müller's (1879) original idea that shared warning signals reduce individual mortality by educating predators more efficiently was made by Rowland et al., (2007) as they conducted an experiment to investigate whether mimicry between unequally defended prey species results in mutualistic or parasitic interactions. The study tested the predictions of Müllerian mimicry theory using a controlled "novel world" environment in which wild-caught great tits (*Parus major*) served as naive avian predators. Prey types included highly defended models, moderately defended prey – perfect and imperfect mimics and palatable Batesian mimics. They found out that increasing the number of edible Batesian mimics had nuanced effects on predation outcomes. Although the mortality of the defended model species remained unchanged when more mimics were added, the edible mimics themselves experienced a notable decrease in mortality when they were presented alongside models (Rowland et al., 2007). This suggests that mimics benefit from the presence of defended species through association. Comparisons showed that mimics survived better when paired with models than when they were alone, though increasing the number of mimics beyond a certain point did not offer additional protective benefits. However, results also revealed that increasing the abundance of moderately defended mimics led to a significant decrease in the per capita mortality of both the model and the mimics themselves. This effect occurred regardless of whether the mimicry was perfect or imperfect, although imperfect mimics suffered higher overall mortality, indicating selection pressure favouring perfect mimicry (Rowland et al., 2007). Importantly, the presence of mimics did not induce increased attacks on the model when the overall density was accounted for. Instead, both species benefited from shared predator education, aligning with Müllerian mimicry predictions. The birds consumed more of the moderately defended mimics than the highly defended models when presented alone, confirming that predators distinguish between different defence levels. In conclusion, Rowland et al. (2007) provided experimental evidence that unequally defended co-mimics can experience mutualistic benefits, particularly at higher densities. This finding directly challenges theoretical models predicting parasitism in such systems (Rowland et al., 2007).

In contrast, an earlier research of Speed et al. (2000) showed reverse results as they conducted an experiment to test predictions of Müllerian and Batesian mimicry under natural predation conditions. The researchers constructed pastry “prey” and dyed them with food colouring. Three prey types were created: first, highly defended (unpalatable) prey as model, second - moderately defended prey as mimic, and as last edible control. The study included wild birds, primarily European blackbirds, starlings, along with sparrows and robins. The density of moderately defended prey was varying while the number of highly defended prey remained constant. Data collected on the number of each prey type attacked revealed that as the density of moderately defended prey increased, the per capita attack rate on the highly defended prey also increased (Speed et al., 2000). This outcome is consistent with unconventional mimicry theories predicting quasi-Batesian interactions, whereby an abundance of moderately defended mimics dilutes the protection afforded to better defended models. The studies by Rowland et al. (2007) and Speed et al. (2000) offer contrasting insights into mimicry between unequally defended species. Rowland et al. (2007) found that moderately defended mimics can reduce predation on both themselves and highly defended models, supporting mutualistic Müllerian mimicry. However, Speed et al. (2000) showed that increasing mimic density in the wild raised attack rates on the model, consistent with quasi-Batesian parasitism. These opposing results suggest that survival rate of mimics and models depend on ecological context, prey density and predator experience (Speed et al., 2000).

Rowland et al. (2010) expanded previous experiment conducting a controlled laboratory study to examine whether mimicry between unequally defended prey species is always mutualistic, as in classical Müllerian mimicry, or whether it can become parasitic, supporting the hypothesis of quasi-Batesian mimicry. The research employed wild-caught great tits (*Parus major*) as visually hunting predators, and artificial prey constructed from almonds designed to differ in edibility: cryptic edible prey, moderately defended prey soaked in a low concentration of chloroquine phosphate, and highly defended "model" prey soaked in a higher concentration. Results showed that predators did not distinguish between the model and mimic prior to attack, confirming that visual mimicry was effective. (Rowland et at., 2010). Importantly, as the frequency of the mimic increased, so too did the per capita predation rate on the model–mimic pair. Mimicry thus failed to reduce risk and instead imposed a cost on the better-defended model, consistent with parasitic mimicry, which correlates with study of Speed et al. (2000) with wild birds. When mimics were rare, they gained protection without increasing risk to the model, supporting the idea of effectively neutral mimicry. However, at high mimic frequencies both mimic and model faced elevated predation. To investigate state-dependent foraging, the authors manipulated birds' physiological state by pre-feeding them mealworms injected with either water or chloroquine. When birds were toxin-laden, they avoided common mimics more than rare ones. This supports the view that predators trade off nutritional value and toxicity, adjusting decisions based on their internal state. Rowland et al. (2010) also investigated how the relative frequency of a mimetic versus a non-mimetic form of a moderately defended prey species influences survival under predation. When mimics were absent, the non-mimetic form served as a baseline for comparison. At low mimic frequency, there was no clear survival difference between forms. However, at intermediate frequency, mimics showed significantly better survival than non-mimics, indicating a protective benefit from resembling the highly defended model Rowland et al., 2010). The study overall concludes that mimicry between unequally defended prey is not inherently mutualistic. Instead, mimicry may be parasitic or neutral depending on the mimic's frequency but also presence of non-mimetic prey and predator's physiological state. This supports the theoretical concept of quasi-Batesian mimicry and provides empirical evidence under tightly controlled conditions (Rowland et al., 2010).

An experiment of Barnett et al. (2014) aimed to investigate how birds respond to prey with variable levels of toxicity, using European starlings (*Sturnus vulgaris*) as the test subjects. The starlings were trained to flip paper lids off Petri dishes containing mealworms that varied in toxin levels. Three types of prey were presented: undefended mealworms, fixed defence mealworms (injected with a constant amount of quinine), and mixed defence mealworms (half injected with water and half with quinine). Both the fixed and mixed defence prey had the same average toxin level, but the mixed defence prey had variability in toxin content, whereas the fixed-defence prey had a consistent toxin level. Over ten test sessions, birds were observed to be less likely to consume mixed-defence prey compared to fixed-defence prey, even though the mean toxin levels were similar between the two. Additionally, the likelihood of birds eating either defended prey type decreased as the presentation number within a session increased (Barnett et al., 2014). The results suggested that variability in toxin levels (mixed defence) made the prey more aversive to predators, as birds avoided it more than consistently defended prey, even though the average toxin intake was similar. This indicates that predators may find variable defence prey aversive, supporting the idea that variability in toxin levels can be an adaptive strategy for prey (Barnett et al., 2014).

The experiments collectively illustrate the dynamic nature of mimicry outcomes, emphasizing the importance of chemical diversity, prey density, and predator state. Barnett et al. (2014) demonstrated that avian predators avoid variably defended prey more than prey with consistent toxin levels, indicating that unpredictability in chemical defence increases aversion. This aligns with findings by Skelhorn and Rowe (2005), who found out that chicks avoided red crumbs more effectively when they were laced with two chemically distinct toxins, suggesting that chemical diversity enhances avoidance learning. However, Skelhorn and Rowe (2006) found no such advantage when visual signals also varied, proposing that visual distinctiveness may override chemical cues. Rowland et al. (2007) expanded on Müllerian mimicry theory, showing that moderately and highly defended prey can both benefit from shared signals under predator education, but their later study (2010) revealed that high mimic frequency could impose costs on the model, particularly when predators' internal toxin loads were manipulated, supporting quasi-Batesian dynamics. In contrast, Speed et al. (2000) showed that increasing mimic density in natural conditions elevated attack rates on the model, indicating parasitism.

4.1.2 Frequency-dependent Selection

The frequency-dependent selection theory in predator interactions with mimics was first introduced by Turner (1970) based on his empirical observations. He proposed that the survival of mimics is contingent upon their frequency relative to models. When mimics are rare, predators learn to avoid the warning signal through repeated aversive encounters with toxic or otherwise defended prey. However, if mimics become too abundant, predators may sample more often, reducing the effectiveness of the aposematic signal (Turner, 1970).

Huheey (1980) investigated how the frequency of model and mimic species within a prey population affects predator behaviour, supporting a frequency-dependent model of predation. He predicted that the effectiveness of mimicry is influenced by the relative abundance of models: predators learn to avoid models based on negative experiences and then generalize this avoidance to mimics, with this learning being frequency sensitive. Species involved in the study included two amphibian predators: the southern toad (*Bufo terrestris*) and the green tree frog (*Hyla cinerea*). The prey consisted of honeybees (*Apis mellifera*), with intact bees used as noxious models (sting-equipped) and modified bees (sting and venom sac removed) serving as mimics. This design removed additional variables such as buzzing sounds, allowing for a clean comparison of visual mimicry effects. The experimental method involved individually housing the predators and presenting them with bees in randomized sequences at varying model frequencies. The frequency of mimic consumption was recorded and analysed using a mathematical model introduced by Huheey (1964), which incorporates a parameter n representing the predator's "memory" span, or more accurately, its risk-avoidance behaviour after a negative experience. Results showed that as the proportion of models increased, the overall predation rate on the prey population decreased, as strong evidence for frequency-dependent avoidance (Huheey, 1980).

Finkbeiner et al. (2018) investigated how frequency-dependent selection influences avian predator behaviour in the context of imperfect Batesian mimicry. They conducted field experiments on two sites using two butterfly species from the *Adelpha* genus: *Adelpha iphiclus*, the presumed unpalatable model, and *Adelpha serpa*, a putative palatable mimic. On first site where mimic and model occurred at similar frequencies, predators significantly discriminated between the two, with *A. serpa* suffering higher predation than *A. iphiclus*. (Finkbeiner et al., 2018). This indicates a breakdown in mimicry likely caused by an unfavourable mimic-to-model ratio. By contrast, on site two, where *A. iphiclus* was more abundant than *A. serpa*, the species experienced similarly low predation rates, suggesting that the mimic gained protection via association with the common model, despite slight imperfections in its appearance (Finkbeiner et al., 2018). These results support theoretical predictions of frequency-dependent selection in mimicry , when mimics become too frequent relative to models, predators are more likely to detect and target them, diminishing the protective benefits of mimicry. Conversely, rare mimics benefit from generalized predator avoidance of the common model (Finkbeiner et al., 2018).

More empirical evidence was made by He et al. (2022) as they investigated in their field experiment how avian predator behaviour, specifically taste-rejection, responded to varying frequencies of mimics within mimetic prey systems. In deceptive mimicry, undefended mimics imitate the warning signals of toxic models, increasing their own survival but also potentially increase predation risk for the models. When mimic frequencies approach 50%, uncertainty for predators is highest, as visual cues become unreliable in predicting chemical defences. In such situations, predators are expected to engage in "taste sampling," catching and then rejecting unpalatable prey to gather more reliable information (He et al., 2022). They demonstrated that mimic frequency strongly influences avian predator responses, particularly in terms of taste rejection behaviour. The highest rates of taste rejection occurred at intermediate mimic frequencies, where the reliability of visual warning signals was lowest, supporting the prediction that signal ambiguity increases predator sampling. When accounting for relative taste rejection, one tested site exhibited the expected pattern, while other showed a decrease in rejection as mimic frequency increased (He et al., 2022). This divergence suggests regional differences in predator behaviour, potentially influenced by environmental factors or predator community composition. The absence of significant taste rejection in control prey on the first site, but not the second, further underscored these site-specific dynamics. Overall, the results highlighted the importance of mimic frequency and predator learning in shaping the evolutionary dynamics of mimicry systems. These findings contributed to a deeper understanding of how imperfect mimicry can persist in nature and suggest that predator cognition and ecological context are critical factors in the maintenance of mimicry polymorphisms (He et al., 2022).

Altogether, these studies demonstrate that frequency-dependent selection is a key driver in the evolution and maintenance of mimicry systems. Turner (1970) first proposed that mimic survival depends on their frequency relative to models: rare mimics are protected by predator avoidance of defended models, but high mimic abundance undermines this effect. Huheey (1980) confirmed this with amphibian predators, showing that mimicry is more effective when models dominate, due to predator learning and memory. Finkbeiner et al. (2018) and He et al. (2022) revealed that predators adjust their responses based on the reliability of warning signals, which depends on mimic-model ratios. All studies agree that mimicry functions best when mimics are rare and models common. However, He et al. (2022) observed site-specific differences, suggesting that predator behaviour and ecological context can modify the expected outcomes. Thus, while the mechanism is broadly supported, its expression varies across environments.

4.1.3 The Presence of Alternative Prey

The presence of alternative prey is a critical factor influencing the stability and efficacy of mimicry systems. Alternative prey, defined as palatable or otherwise profitable prey items available alongside mimetic or aposematic species, affect predator foraging decisions by modulating perceived risk and reward. When alternative prey is abundant, predators are more likely to avoid uncertain or potentially defended prey, thereby reinforcing mimicry. Conversely, when alternative prey is scarce, predators are more likely to sample aposematic or mimetic prey, potentially undermining signal reliability and increasing the risk to both models and mimics. Servedio (2000) presented mathematical model describing the abundance and diversity of alternative prey can significantly affect predator decision-making, particularly by reinforcing or weakening aversion to mimetic species. In Batesian systems, this dynamic determines whether mimics thrive or fail. The presence of alternative prey not only buffers predator risk but also supports the ecological stability of mimicry rings and mimic-model systems, especially under variable conditions of predator learning and prey toxicity (Servedio, 2000).

Experiment with wild caught great tits (*Parus major*) by Lindström et al. (2004) demonstrated that predator foraging behaviour is not static but shifts in response to prey community composition. Lindström et al. (2004) investigated how alternative prey affects Batesian and Müllerian mimicry dynamics, dividing them in 2 separate experiments. In the Batesian mimicry experiment, birds were given a choice between palatable imperfect mimics and unpalatable models. Birds successfully learned to avoid models while reducing the availability of alternative prey lowered the effectiveness of mimics. Next results showed that encounters with mimics were more randomized when the alternative prey was abundant and predation of imperfect mimics decreased a bit, suggesting that even imperfect mimicry might be slightly beneficial (Lindström et al., 2004). In the Müllerian mimicry experiment, both models and mimics were unpalatable, with the models treated with a higher chloroquine concentration. Birds responded more strongly to visual cues than to taste differences when distinguishing between unpalatable prey. Colour played a dominant role in predator decision making, with green-coloured prey avoided more rapidly than blue-coloured prey, indicating that green served as a stronger warning signal and was more likely to function as the model within this experimental system. Both prey types were rendered unpalatable using chloroquine and benefitted from their distastefulness from the start of the trials, but the availability of alternative prey influenced how quickly birds learned to avoid them since they learned faster about the unpalatability of models when alternative prey was abundant (Lindström et al., 2004). However, birds attacked models proportionally to their frequency, suggesting no preference based solely on the presence or absence of alternatives. This indicates that, unlike Batesian mimicry systems where mimic survival increases with more abundant alternative prey, Müllerian co-mimics experience similar levels of predation regardless of the availability of other food sources (Lindström et al., 2004).

Lindström et al. (2004) provided empirical support for Servedio's (2000) theoretical predictions about alternative prey and mimicry stability. Servedio's models showed that abundant, palatable prey make predators more risk-averse, thereby reinforcing avoidance of defended or uncertain prey and allowing Batesian mimics to thrive; conversely, scarce alternative palatable prey force predators to sample mimics and models more often, undermining signal reliability. Lindström's experiments with great tits confirmed these dynamics: when alternative prey was plentiful, Batesian mimics were protected but when alternatives were scarce, mimic attack rates went higher (Lindstrom et al., 2004).

4.1.4 Trade-offs Between Nutritional State and Toxic Load

Previously noted in Introduction, Barnett et al. (2007) conducted a controlled laboratory experiment to investigate whether the energetic state of educated predators influences their willingness to consume chemically defended prey. Using European starlings (*Sturnus vulgaris*), the researchers tested the birds' foraging behaviour when offered palatable and unpalatable prey under two different energetic conditions: free-fed and food-restricted. The prey used in the experiment were live mealworms (*Tenebrio molitor*), prepared in two conditions: undefended mealworms injected with water, and defended mealworms injected with a quinine sulphate solution, which made them distasteful. The key finding was that birds consumed significantly more defended prey when in a food restricted state compared to when they were free fed (Barnett et al., 2007). While the number of undefended prey consumed remained consistently high in both conditions, defended prey consumption increased in the restricted condition. This difference demonstrates that the birds adjusted their foraging strategy according to their energetic needs, tolerating the cost of ingesting toxins when their energy reserves were low (Barnett et al., 2007). To ensure that this behaviour was not the result of reduced cognitive ability or indiscriminate foraging under energy stress, the researchers conducted a series of simultaneous choice trials at the end of the experiment. The results confirmed that even when food restricted, birds retained their learned discrimination between colour cues and continued to prefer undefended prey when visual cues were available (Barnett et al., 2007). When colour cues were removed and only chemical differences remained, birds showed no preference, indicating that visual learning was the primary basis of discrimination. These results support the idea that educated predators strategically balance the energetic benefits of consuming prey against the physiological costs of ingesting toxins (Barnett et al., 2007). Rather than completely avoiding aposematic prey, as classical models of predator learning would suggest, birds modulated their behaviour based on their current energetic state. This supports theoretical models of state-dependent foraging, such as those proposed by Sherratt (2003), and suggests that asymptotic attack rates on defended prey are not fixed but flexible depending on internal conditions.

Sherratt (2003) developed a stochastic dynamic programming model to examine how predator's energetic state affects attack rates on chemically defended prey. Traditional models assume that predators behave uniformly, always avoiding unprofitable prey. However, he argued that such models overlook a crucial ecological factor: predators face a trade-off between avoiding toxic prey and staving off starvation. His model explicitly quantified this trade-off and predicted predator behaviour based on varying levels of hunger and prey availability (Sherratt, 2003). He showed that predators were significantly less likely to attack defended prey when alternative palatable food was abundant. This dietary conservatism emerged not from risk aversion but from survival-maximization strategies. Increasing the density of undefended mimics, while holding model density constant, led to a decrease in attacks on both mimics and models, as a contrary to expectations under traditional mimicry theory (Sherratt, 2003). This occurs because the abundance of non-toxic prey helps sustain predators, reducing the need for risky foraging behaviour. By integrating predator state into the evolutionary logic of warning coloration and mimicry, Sherratt's model provided a compelling explanation for the persistence of imperfect mimics in nature and challenged the binary classification of mimicry into strictly Batesian or Müllerian categories (Sherratt, 2003). Barnett et al. (2007) and Sherratt (2003) show that predator responses to defended prey are flexible and influenced by hunger and prey availability. Rather than consistently avoiding toxic prey, predators adjust their behaviour based on energetic need, supporting state-dependent foraging theory. This corresponds with the research of Rowland et al. (2010) as in their experiment, predators adjusted their choices based on toxin load, avoiding common mimics when already toxin laden (Rowland et al., 2010). This highlights a trade-off between nutritional value and toxicity and challenges traditional mimicry models, suggesting that mimicry dynamics are more context dependent and less rigid than previously assumed (Sherratt, 2003).

Skelhorn et al., (2016) summarized knowledge about predator behaviour in asymptotic phase based on empirical evidence of multiple authors but also described their experiments designed to explore how predators, specifically European starlings (*Sturnus vulgaris*) learn about and make foraging decisions regarding interactions with aposematic prey. They confirmed that birds can learn about toxicity and balance their physiological needs based on their condition (Skelhorn et al., 2016). Skelhorn et al. (2016) further discussed an intake of toxic prey during the early "acquisition phase," forming an association between the prey's signal and the adverse effects of toxins, which includes learning about prey defence rather than its complete avoidance (Skelhorn et al., 2016). It is proposed that the most significant findings about the phenomenon emerge during the "asymptotic phase," where predators do not entirely avoid toxic prey. Instead, predators make state-dependent decisions, increasing their attacks on toxic prey when they are energetically stressed, in cold conditions, or have limited access to nutritious alternatives (Skelhorn et al., 2016). Predators also decrease attacks when they have a high existing toxin burden, suggesting a physiological regulation of risk. Moreover, when toxic prey is nutritionally enriched, birds are more likely to include them in their diets, demonstrating that predators can learn about both toxin and nutrient content and weight these factors adaptively (Skelhorn et al., 2016). The conclusion is that predator foraging decisions are not static outcomes of aversion learning but are dynamic and strategic, influenced by internal physiological states, external environmental conditions, and information previously gathered about prey profitability (Skelhorn et al., 2016).

Together, these studies demonstrate that predator responses to chemically defended prey are shaped not only by learned aversions but also by internal states such as hunger and toxin burden. Barnett et al. (2007), Rowland et al. (2010) and Skelhorn et al. (2016) each highlight a key trade-off predators face between nutritional gain and the cost of ingesting toxins. Predators do not uniformly avoid toxic prey but instead modulate their foraging strategies according to energetic need, environmental conditions, and prior experience. These findings support Sherratt's (2003) theoretical model of state-dependent foraging and challenge the traditional view of aposematism as a simple avoidance mechanism and emphasize the complexity of predator cognition, with important implications for understanding the evolution of warning signals, mimicry, and prey defence strategies.

4.2 Examples of Mimicry Rings and Mimicry Complexes

Müllerian mimicry ring is formed by two or more unpalatable species sharing similar aposematic signal (Turner, 1970). One of the best-known examples of Müllerian mimicry rings are *Heliconius* butterflies, *Heliconius erato* and *Heliconius melpomene* (Turner, 1970). The species mentioned have nearly perfect resemblance to each other and are equally toxic which makes the predators avoid them. When a wider number of species varying through taxa share similar phenotype, they create a mimicry complex. Based on the species included in the spectrum, a mimicry complex can be Müllerian or even Batesian-Müllerian as the group may include undefended mimics too (Williams, 2007; Wilson et al. 2015 as cited in Pekár et al., 2017).

Chouteau et al. (2019) explored predator learning in response to chemical defences across a diverse set of mimetic butterflies from northeastern Peru. Central to this investigation was a detailed analysis of the mimetic communities involved, thirteen chemically defended species from three taxonomic clades (*Heliconiinae*, *Danainae*, and *Pericopinae*) participating in six distinct mimicry rings. These mimicry rings were defined by their shared aposematic visual patterns, which evolved through Müllerian mimicry mutualistic convergence (Choteau et al., 2019). The *Heliconiinae* subfamily, particularly the genus *Heliconius*, was most prominent in the study. These butterflies are chemically defended by cyanogenic glycosides, which they either sequester or biosynthesize. Cyanogenic glycosides release toxic cyanide compounds when consumed, offering effective deterrence against predators and playing a crucial role in Müllerian mimicry by promoting avoidance learning (Choteau et al., 2019). The *Danainae* subfamily utilizes a different chemical defence strategy, relying on pyrrolizidine alkaloids, which they acquire from host plants during their larval stages. These alkaloids are toxic to predators, causing liver damage and acting as an effective deterrent. The *Pericopinae* subfamily, represented by *Chetone histrio* and *Chetone hydra*, also employs pyrrolizidine alkaloids for defence, similar to the *Danainae*, although the specific compounds were not confirmed in the study. In contrast, the non-mimetic species *Anartia amathea*, which lacks chemical defences, served as a baseline control, demonstrating how chemical defences enhance predator learning and avoidance behaviour (Choteau et al., 2019) This diverse set of species highlights the important role chemical defences play in the evolution and stability of mimicry complexes, ensuring mutual protection among co-mimics in predator-rich environments. The experiment utilized domestic chicks (*Gallus gallus domesticus*) as model predators. The researchers prepared experimental crumbs by grinding the bodies of the butterflies and mixing them with chick feed. The crumbs were dyed in two different colours to dissociate visual cues from chemical ones, allowing the researchers to isolate the effects of chemical defence on predator learning. Over time, chicks began to show a clear preference for the control crumbs, reducing their consumption of the experimental ones (Choteau et al., 2019). This decrease in consumption was interpreted as avoidance learning, with the chicks associating the toxic properties of the experimental crumbs with an unpleasant experience. The learning rate varied among species, with some species inducing rapid avoidance learning, such as *Heliconius sara* and *Heliconius aoedes*, while others, like *Mechanitis polymnia* and *Eueides isabella*, prompted slower learning (see Chouteau et al., fig. 2).

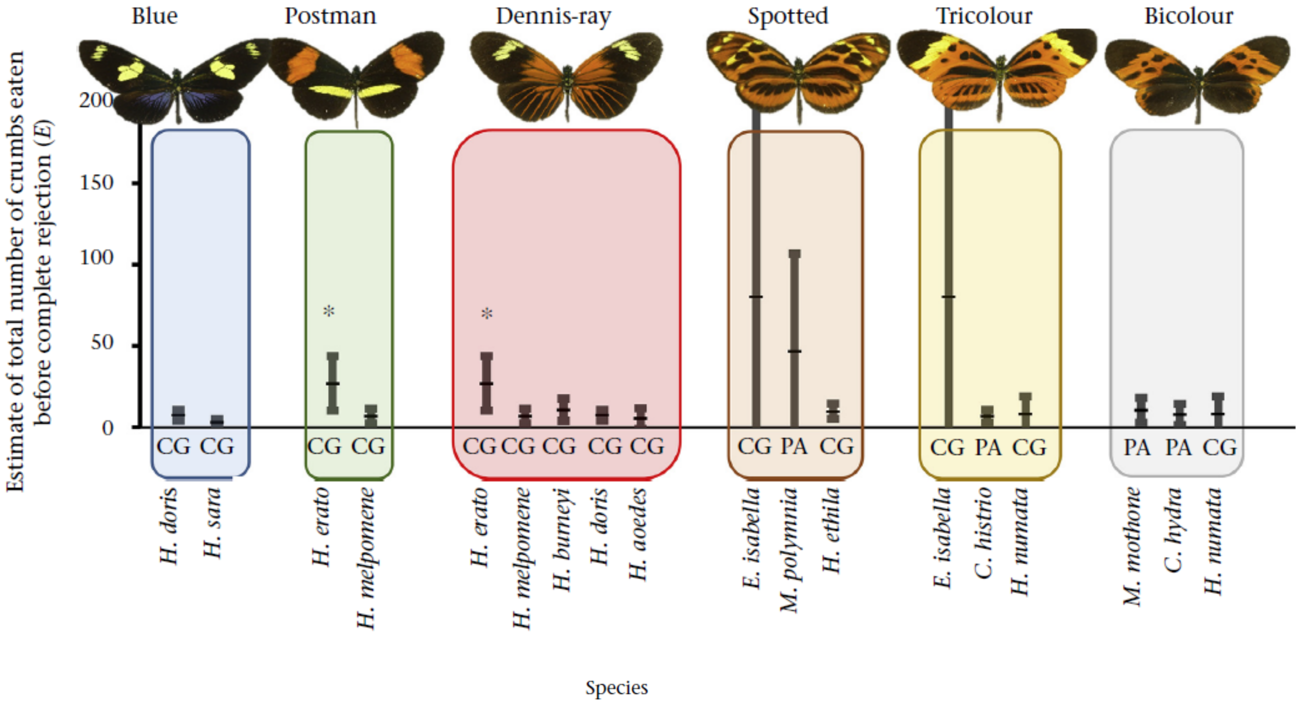

Figure 2. Variation in predator avoidance learning generated by species within and across mimicry rings. Species showing significant differences in the rate of avoidance learning (mean E and 95% confidence interval) from all of their co-mimics (or one mimic; horizontal bar) are indicated with asterisks: $^{*}P = 0.10$; $^{**}P = 0.05$. The coloured regions in the graph delimit the species' mimicry rings, and the butterfly images denote mimetic warning signals. Chemical identity of defences is indicated for each species: CG = cyanogenic glycosides; PA = pyrrolizidine alkaloids.

However, beyond a certain toxin threshold, further increases in toxicity did not improve avoidance rates regardless of type of chemical compound. This suggests that once butterflies reach moderate level of chemical defence, an additional toxicity is not relevant for lowering predator attacks. Choteau et al. (2019) found out that there is a significant variation in the rate of avoidance learning among species, even within the same mimicry rings, suggesting that factors beyond just the chemical defence contributed to the predators' ability to learn to avoid certain prey. They also pointed out that when predators cannot readily distinguish prey species within a mimicry ring based on visual signals, then the most defended species contribute similarly to effectiveness of a mimicry ring (Choteau et al., 2019).

Pekár et al. (2017) published study describing “golden mimicry complex.” During the research, they analysed at least 140 putative mimics from four arthropod classes including ants, wasps, bugs, tree hoppers and spiders and recorded multiple interactions with predators. The golden mimicry complex includes species which are sharing conspicuous golden body markings (Pekár et al., 2017). The study highlighted how multiple defensive traits, including structural and chemical defences which contributed to predator aversions. Predators, regardless of visual or non-visual sensitivity, avoided golden coloured mimics, suggesting that the golden coloration is an effective deterrent communicated through various sensory modalities. The research revealed that mimics, even with less intense defences, experienced lower predation pressure compared to non-mimetic species, supporting the idea that mimicry itself provides protection by resembling unpalatable species (Pekár et al., 2017). Predator guilds, including both birds and reptiles, exhibited a stronger avoidance of mimics, with predation rates unaffected by the degree of unpalatability. This suggests that the protective effect of mimicry outweighs the specific defence level of the species. Interestingly, moderately defended species was most prevalent in the mimicry rings, benefiting from the collective protective signal of the complex. The study also emphasized the role of non-visual signals like vibrations and chemical cues in predator avoidance, with non-visual predators also avoiding golden mimics (Pekár et al., 2017).

In another field study, Hlaváček et al. (2022) focused on possible first-model scenario, observing Batesian-Müllerian mimicry ring centred around *Vespa orientalis.* In first-model scenario, model species emerge earlier in the season than mimics and as a result of that, naive predators learn to associate the warning signal with unpalatability first. This allows mimics to benefit from the already developed aversion to the model's appearance. In this case, five hymenopteran species were classified as Müllerian mimics, while three dipteran species as Batesian mimics. The study indeed provided support for the ‘model-first’ scenario, where the model species, *V. orientalis*, emerges earlier in the season, setting the timing for the mimics (Hlaváček et al., 2022).

Not only terrestrial organisms are observed to form mimicry complexes. Winters et al. (2018) studied aposematic seawater molluscs located along the east coast of Australia, partially focusing on a putative red dot mimicry ring containing species characterized by their red spots and/or distinctive yellow/orange mantle borders (Winters et al., 2018). Measuring the chemical defence was based on mortality of brine shrimp *Artemia salina* nauplii cultivated on a Petri dish together with nudibranch tissue, revealing that *G. tasmaniensis, H. benneti* and *M. festiva* inflict over 50 % mortality of shrimps and therefore can be classified as toxic, lower level of chemical defence was then observed on *G. daphne* with mortality under 50 %. On the other hand, *G. tinctorius* and *G. splendidus* extracts did not affect shrimp mortality at all and could be Batesian mimics, although, when testing their edibility by Rock Pool shrimp *Palaemon serenus*, all species appeared to have at least partial antifeedant response, supporting they might be distasteful and therefore considered quasi-Batesian mimics (Winters et al., 2018). Toxins were produced mainly through metabolites. This study provides quantitative evidence of visual similarities among species within a putative mimicry group, showing that shared colour and pattern elements distinguish them from closely related species. It is suggested that weakly defended mimics may still benefit from resembling more toxic models, as predators may not be able to differentiate toxicity based on distastefulness alone (Winters et al., 2018).

In conclusion, the studies on mimicry, including those by Chouteau et al. (2019), Pekár et al. (2017), Hlaváček et al. (2022), and Winters et al. (2018), collectively highlight the dynamic and context-dependent nature of mimicry complexes, where both visual and chemical defences play crucial roles. Chouteau et al. (2019) demonstrated that once a moderate threshold of toxicity is reached, additional chemical defence does not significantly enhance predator avoidance, regardless of the compound type. While well-defended species generally contribute equally to the effectiveness of mimicry rings, particularly when predators cannot distinguish between co-mimics, there was still significant variation in predator learning rates among species. Pekár et al. (2017) showed that even weakly defended mimics benefit from visual resemblance within a mimicry complex, reducing predation pressure. This suggests that the visual aspect of mimicry, even in the absence of potent chemical defences, provides substantial protection against predators, supporting the idea that mimics gain a collective advantage by resembling unpalatable species. Similarly, Winters et al. (2018) observed that weakly defended mimics might still benefit from mimicry, as predators may struggle to differentiate between toxic and non-toxic species.

4.3 Polymorphic Mimicry Systems

Some mimics have evolved an advanced form of protection, being able to resemble not only one model, but two or more. *Ranitomeya imitator*, a Müllerian mimic native to Peru, is quite spectacular example of divergence. Documented by Twomey et al. (2016), this poison dart frog imitates 4 different species, which might lead in ecological speciation and development of a reproductive barrier by the time (there is no reproductive barrier confirmed so far). Forming a mimicry complex, the morphs are based on different locations of model species. Apart from that, areas called transition zones are characteristic for the morphs with hybrid pattern present, changing from one form to another (see Twomey et al., 2016 fig. 1).

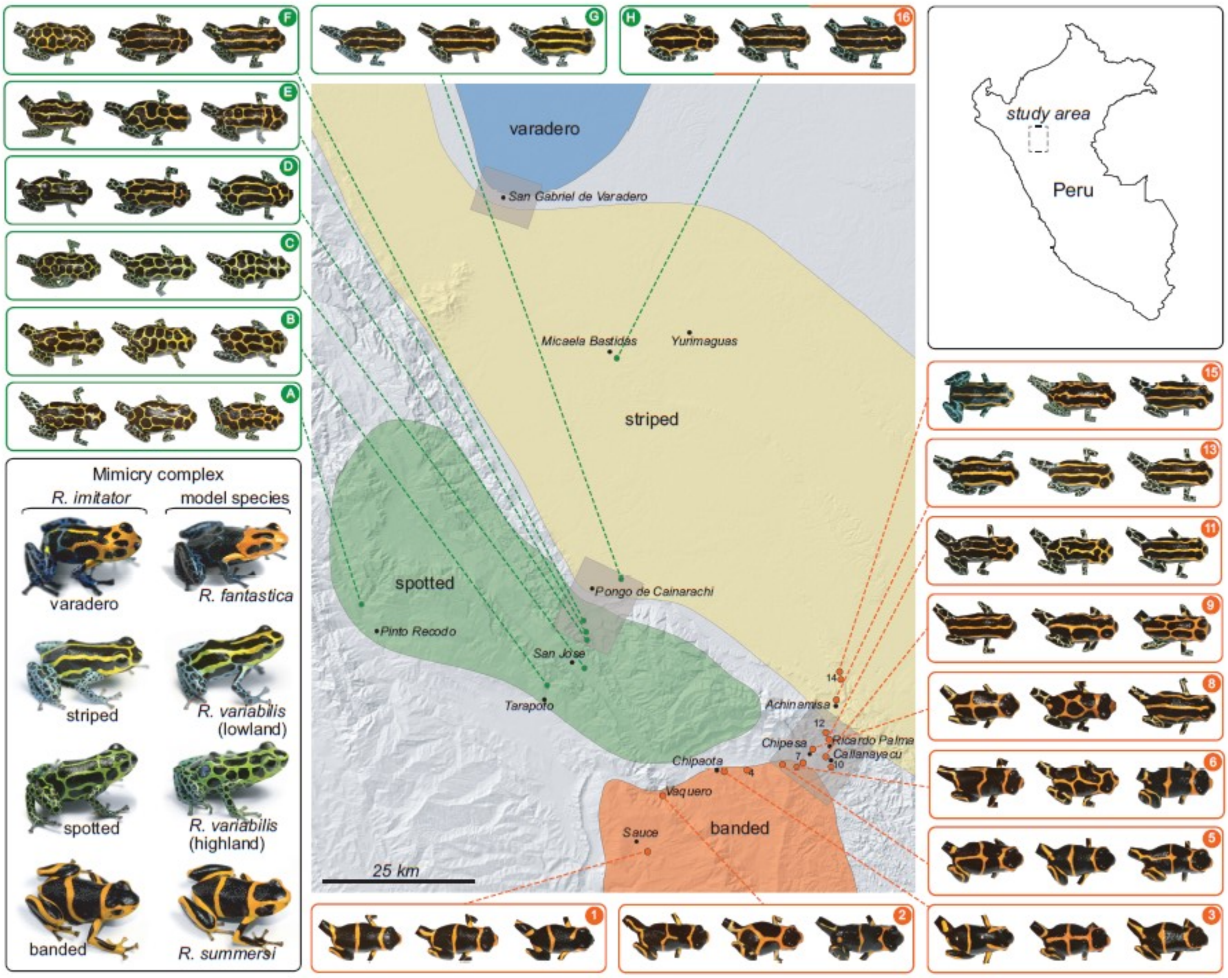

Figure 1: Müllerian mimicry and variation in *Ranitomeya imitator*. Lower left: Depiction of the mimicry complex, showing four mimetic morphs of *R. imitator* and corresponding model species. Upper right: Map of Peru showing study area. Center: geographical distribution of mimetic morphs of *R. imitator* and sampling localities. Orange dots show *R. imitator* populations included on the banded-striped transect; green dots show *R. imitator* populations included on the spotted-striped transect; black dots represent towns. Population numbers/letters correspond to tables A1 and A2, available online, respectively. Note that the Micaela Bastidas population (population H/16) is included in both transects. The gray boxes show the three mimetic transition zones studied here. Note that the spotted and banded morphs come into close contact but do not form a transition zone, which is apparently due to geographic isolation from the Huallaga River.

The defence against predators is based on toxic alkaloids frogs most likely obtain by eating poisonous arthropods, so they later secret batrachotoxin through their skin (Zaaijer & Groen, 2024). An aposematic signal of a dart frog is often composed of contrasting patch against the dark background, usually located at dorsal, together with bright coloured femoral skin (Amézquita et al., 2017). Not every species has such markings though, for example, *Phyllobates terribilis* frog's body is whole bright coloured and divided in 3 morphs, from yellow to mint green and orange. Amézquita et al. (2017) during their research of mimetic complex in *Allobates femoralis,* both Batesian and Müllerian mimics, found out that even though femoral skin is the most contrasting body part, the model-mimic resemblance is highest in dorsal area. Thus, they suggested the markings might have more surviving strategies, such as disruptive coloration from distance and aposematic signal when predators approach the prey closer (Amézquita et al., 2017).

Kuchta et al. (2008) studied polymorphic salamander *Ensatina eschscholtzii,* which has an aposematic form *E. e. xanthopica,* suggesting a Batesian mimicry linked to highly poisonous pacific newts from genus *Taricha*. Tested model, *Taricha torosa* newt has brown dorsal and bright spectre of red to orange tone ventral body coloration, with conspicuous yellow eyes. Compared to *E. e. xanthopica*, the pattern looks a lot alike but a distinct difference between them are their body shapes as the *E. e. xanthopica's* head is a lot more narrow. Hence, this strongly supports the Batesian mimic hypothesis, especially when we consider there are other 6 subspecies and all of them possess either cryptic or disruptive coloration (Kuchta et al., 2008). Tested on wild caught birds, western scrub-jays (*Aphelocoma californica*), they exposed *Taricha* newts to the predators first and no amphibian was consumed in all attempts, though 3 of them were attacked. Shortly after, they observed that in just 5 out of 10 cases, the *E. e. xanthopica* salamanders were eaten, compared to 9 out of 10 consumed control species *E. oregonensis*, the non-mimetic subspecies of *Ensatina* genus, which suggests Batesian mimicry relationship rather than Müllerian, though more study is required (Kuchta et al., 2008).

5 Conclusions

Key theoretical models, particularly those introduced by Turner (1984) Speed (1993), and Balogh et al. (2008) underscore the importance of predator behaviour, learning, forgetting, and decision-making within ecologically realistic contexts. These models highlight that the protective value of mimicry can shift based on mimic abundance, toxin variability, or presence of alternative prey. Empirical studies with avian predators further support these predictions, demonstrating that unequally defended mimics can sometimes reduce, and at other times enhance, the protection afforded to models.

A consistent pattern emerging from the data is the role of variability: whether in chemical defence levels, predator state, or environmental context. Studies examining state-dependent foraging strategies indicate that predators may consume mildly defended prey when energetically stressed, supporting the view that mimicry relationships are not fixed but shift along a spectrum of mutualism to parasitism. Moreover, polymorphism and mimicry rings across insects, amphibians, and even marine molluscs, highlight the ecological and evolutionary plasticity of mimicry systems.

In conclusion, quasi-Batesian mimicry illustrates the fluidity of ecological interactions, where mimicry strategies evolve under selective pressures shaped by predator cognition, prey defence, and environmental variability. Rather than static categories, mimicry should be understood as a dynamic continuum shaped by behavioural ecology and the nuanced interplay of defence strategies within complex predator-prey systems.

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