Mimetic resemblance in the butterfly mimicry rings of North-East India

A Thesis

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by

Yangchen Lhamo

Indian Institute of Science Education and Research Pune
Dr. Homi Bhabha Road,
Pashan, Pune 411008, INDIA.

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Supervisor: Dr. Krushnamegh Kunte,
NATIONAL CENTRE FOR BIOLOGICAL SCIENCES, Bangalore
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Certificate

This is to certify that this dissertation entitled 'Mimetic resemblance in the butterfly mimicry rings of North-East India' towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune, represents study/work carried out by Yangchen Lhamo at Indian Institute of Science Education and Research under the supervision of Dr. Krushnamegh Kunte, Associate Professor, National Center for Biological Sciences (NCBS), during the academic year 2024-2025.

Kunte

Dr. Krushnamegh Kunte

Committee:

Dr. Krushnamegh Kunte

Dr. Deepak Barua

This thesis is dedicated to my parents Kesang and Sunita

Declaration

I hereby declare that the matter embodied in the report entitled " Mimetic resemblance in the butterfly mimicry rings of North-East India " is the result of the work carried out by me at the Department of Biology, Indian Institute of Science Education & Research (IISER) Pune, under the supervision of Dr Krushnamegh Kunte and the same has not been submitted elsewhere for any other degree. Wherever others contribute, every effort is made to indicate this clearly, with due reference to the literature and acknowledgement of collaborative research and discussions.

Yangchen Lhamo

Yangchen Lhamo

20201237

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Abstract

Aposematism is a major defensive strategy that deters prey by displaying warning colourations indicating its toxicity. Mimicry is one such example which utilises this concept. Mimicry helps prey survive by resembling the unpalatable or toxic model. This study aims to investigate the extent of mimetic resemblance in the butterfly mimicry rings found in the North Eastern part of the Indian subcontinent. We analysed the mimetic resemblance by comparing the spectral reflectance of colours on the wings of the model and mimic using relative discriminability (D_{mimic}). Relative discriminability had a low value for all the pairs, indicating a great extent of resemblance. The ventral side had a stronger resemblance compared to the dorsal side, but not significantly different across most pairs. This might suggest that the selective pressure acting on both sides is comparable. There were no significant differences in the D_{mimic} values between the two avian visual model systems (UVS and VS), implying that mimicry is similar across both predator vision types. This evolution of broad-spectrum resemblance might provide adaptive benefits to the prey, saving them from the diverse avian predator community. It was also observed that the mimics resembled the female models more closely in a monomorphic model system. This study sheds light on our understanding of factors affecting the evolution of mimicry and its extent in the older mimetic communities of North-East India.

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Contributions

Contributor name	**Contributor role**
Dr. Krushnamegh Kunte	Conceptualization Ideas
Dr. Krushnamegh Kunte, Bhavya Dharmaraj	Methodology
Yangchen Lhamo, Bhavya Dharmaraj	Software
Yangchen Lhamo	Validation
Yangchen Lhamo	Formal analysis
Yangchen Lhamo	Investigation
Dr. Krushnamegh Kunte	Resources
Yangchen Lhamo	Data Curation
Yangchen Lhamo	Writing - original draft preparation
Dr. Krushnamegh Kunte, Yangchen Lhamo	Writing - review and editing
-	Visualization
Dr. Krushnamegh Kunte	Supervision
Dr. Krushnamegh Kunte	Project administration
Dr. Krushnamegh Kunte	Funding acquisition

Chapter 1: Introduction

The Evolutionary arms race between the predator and the prey has given rise to various kinds of survival strategies to avoid being attacked by predators. Some of them use deception like camouflage, which helps them blend with the surrounding environment, making them indistinguishable. Another deceptive strategy includes the presence of tails or eyespots in moths and butterflies, which diverts the attack from the vital part of the organism (Prudic et al., 2015).

In contrast, aposematism is a major defensive strategy in nature where organisms rely on conspicuous signals to warn predators of their unpalatability and toxicity (Poulton, 1890). The predators are initially naive and attack the prey only to realise that they are toxic or venomous. Over time, the predators learn to associate these warning colourations with negative consequences and avoid attacking that species in the future, leading to survival success among those who display such signals (Ruxton et al., 2004). Highly conspicuous species are recorded to be better protected than cryptic species, as the predators quickly learn to avoid the former (Gittleman & Harvey, 1980).

Mimicry is an example of an evolutionary strategy that exploits aposematism, where one species evolves to resemble another to gain certain survival benefits.

Mullerian mimicry is when there is a selection for multiple defended species to share an aposematic signal. The mimics benefit by sharing these warning signals, as the more individuals reinforce these honest signals, the less the predation pressure on the whole community, and fewer individuals die per species while educating the predator (Müller, 1879; Rowland et al., 2010). This convergence accelerates the learning of mutual reinforcement of avoidance behaviour in predators and reduces the individual cost of educating predators and the cost of predation on a single species.

Batesian mimicry is where the palatable and, hence, undefended mimics evolve to resemble the aposematic species (Bates, 1862). The Batesian mimic gains a survival advantage without investing in actual defences at the expense of the model and the predator’s learned avoidance.

In nature, the mimetic species interact with each other and often exist in complex communities known as mimicry rings. Mimicry rings are communities that ideally should possess at least one aposematic, well-defended prey species and one Batesian mimic or at least two Mullerian co-mimics (Kunte et al., 2021). The smallest mimicry ring known contains only two species, but larger rings might contain dozens of species. One of the largest known mimicry rings is that of the velvet ant genus *Dasymutilla,* which consists of 65 species (Wilson et al., 2012).

These mimicry rings are usually formed by the spatiotemporal coexistence of models and mimic species and illustrate the dynamic interplay between species within an ecosystem and how they coevolve in response to selective forces. Mimicry rings serve as an excellent model community for ecological and evolutionary studies, as the species participating in these rings have a well-defined nature, network, and strength of interactions, along with well-defined phenotypes.

Several factors shape these mimicry rings, like the regional filtering, density, frequency-dependent selection, toxicity level and the ring's age (Kunte et al., 2021). A relatively higher number of mimics dilutes the effectiveness of the mimicry as the learning in predators depends on the frequency of its encounters with the aposematic species, if the frequency is smaller than the memory parameter, the predator tends to forget the negative/unpleasant experience (Ihalainen et al., 2007; Rowland et al., 2010). A study shows that Batesian mimics were better protected when they comprised 30-60% of the mimicry ring; after that, the fitness advantage declined rapidly (Brower, 1960).

The effectiveness of mimicry depends on how closely the mimic resembles the model and how distinguishable they are from each other to the predators. If they are distinguishable from the predators, the mimics may evolve more convincing mimicry traits, leading to refinement of mimicry patterns. The predator would further evolve a better sensory system, which would help distinguish between the model and the mimic. This relationship facilitates the prey-predator evolutionary arms race, where the cycle of adaptations and counter-adaptations drives the evolution of both species.

Organisms can use various kinds of modalities to convey an aposematic signal, like visual, chemical, auditory or behavioural cues, making it stand out in their surroundings (Barber & Conner, 2007; Raška et al., 2018). However, visual signals have been studied the most as they serve as primary aposematic cues that the predators can detect from a distance. Therefore, variations in colour play a significant role in aposematic signalling.

Butterflies are a great model for studying mimicry with their vibrant colours and patterns, which are important for communication, mate selection and predator deterrence. Mimicry is not just a superficial resemblance but an important survival strategy for them. Butterflies' primary predators are birds with tetrachromatic vision, which enables some species to perceive colours in the ultraviolet range (300–400 nm)(Cuthill et al., 2000; Osorio et al., 1999). Avian cones also have pigmented oil droplets, which help them narrow their spectral sensitivity, functions leading to better colour discriminability (Stavenga & Wilts, 2014; Vorobyev, 2003). Birds can detect and perceive a greater range of colours than humans; hence, they can also notice subtle differences in colour that might not be visible to human vision (Bennett et al., 1994; Endler & Mielke, 2005a).

The butterfly mimetic communities of the Western Ghats have been well studied and have laid the foundation for understanding the dynamics of mimicry. The species involved in the mimicry rings of Western Ghats are known to have resemblance largely due to shared ancestry and stabilized selection on the aposematic pattern of the sister species (Joshi et al., 2017). Owing to the island biogeography theory, the Western Ghats are also known to have younger and smaller mimicry rings (Joshi et al., 2017).

However, the size of the mimicry ring might be variable at different time points in its evolutionary history. In older rings, the frequency of advergence/convergence might be a more significant factor affecting the species' resemblance. This might stem from the fact that those mimicry rings have undergone a prolonged selection process, allowing more distantly related species to adverge/converge (Kunte et al., 2021).

There have been instances of parallelism and convergence over a long period in ancient mimicry rings involving many ants, spiders, wasps and true bugs (Pekár et al., 2017).

The North Eastern part of the Indian subcontinent has rich biodiversity and habitats ranging from tropical forests to mountainous regions. It has been globally recognized as a biodiversity hotspot due to the region’s high level of endemism and species richness (Myers et al., 2000). Due to the region's varied topography and climatic conditions, it is home to a diverse array of butterfly species, especially originating from the Indo-Burmese region following biogeographic considerations. Due to its origin, the mimicry rings present in the Northeast are older than those of the Western Ghats.

Despite North-east India’s ecological significance, the mimetic communities present there are understudied compared to the Western Ghats. This study helps us understand these interactions within these communities. The extent of resemblance between the model and the mimic and among models themselves provides us with critical insights into the success of mimicry. Using an avian visual perspective, we try to understand how birds, the avian predators of butterflies, perceive these colours and whether they can discriminate between the colours of a palatable and an unpalatable species.

This study will also investigate whether this resemblance differs between the dorsal and the ventral wing surfaces under two different vision models. In Western Ghats, it was seen that the ventral surface had better mimetic resemblance, implying stronger natural selection on that surface (Su et al., 2015). In a monomorphic model system where both sexes of the model species look alike, we also try to see if a mimic species looks more like one of the sexes. Such analyses offer deeper insight into the selective pressures shaping mimicry and help us understand the different aspects of mimetic resemblance in the older butterfly mimicry rings of North-East India.

Objectives:

1. Explore the extent of mimetic resemblance in butterfly mimicry rings of North-East India by comparing their colour from an avian visual perspective.

2. Comparing the colour proximity/ resemblance of the ventral and the dorsal side between a model and a mimic pair.
3. Assessing whether the UV and VS birds put differential selection pressure on the mimetic species.
4. Observing in a mimicry ring with monomorphic models, whether a certain model sex was preferred.

Chapter 2:Materials and Methods

2.1 Study population:

The butterfly mimicry rings in the North Eastern part of the Indian subcontinent were classified according to their phenotypic resemblance, spatiotemporal co-occurrence and some known model–mimic relationships. Mimicry rings are often named after the most common model species present or after the most common genus in the ring.

There are nearly 13 rings in North-East India, with ~80 species participating. However, for this study, due to logistical issues and time constraints, only three rings were taken into consideration. The model mimic relationship of the mimicry rings taken for this study, along with the number of individuals sampled per species, is shown in Table 1. Species with more than three individual measures were considered for further analysis due to statistical reasons. All the specimens used for this project are from the Biodiversity Lab Research Collections at NCBS.

The three mimicry rings used for this study are portrayed in Figures 1,2 and 3. The images are not up to scale and only for representational purposes. The double-headed arrow represents the Mullerian mimetic relationship. The one-sided arrow represents the Batesian mimetic relationship where the dot of the arrow represents the aposematic species, and the arrow points towards the Batesian mimic.

The sexes that look similar have been represented by one image and mentioned underneath that both sexes are involved in the mimicry ring. Few Schedule 1 species couldn’t be portrayed due to a lack of specimen pictures.

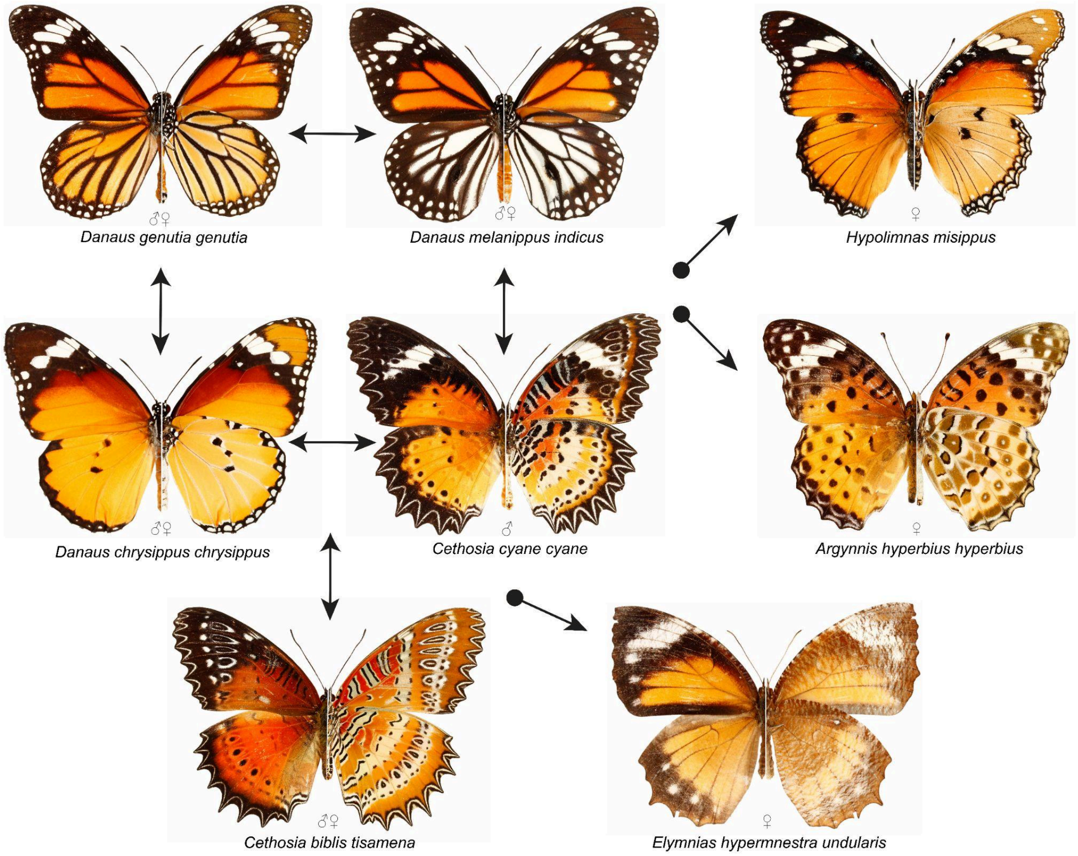


Figure 1: The Danaus mimicry ring with the models and mimics. The left and right sides of the wing represent the dorsal and ventral sides of the butterfly.

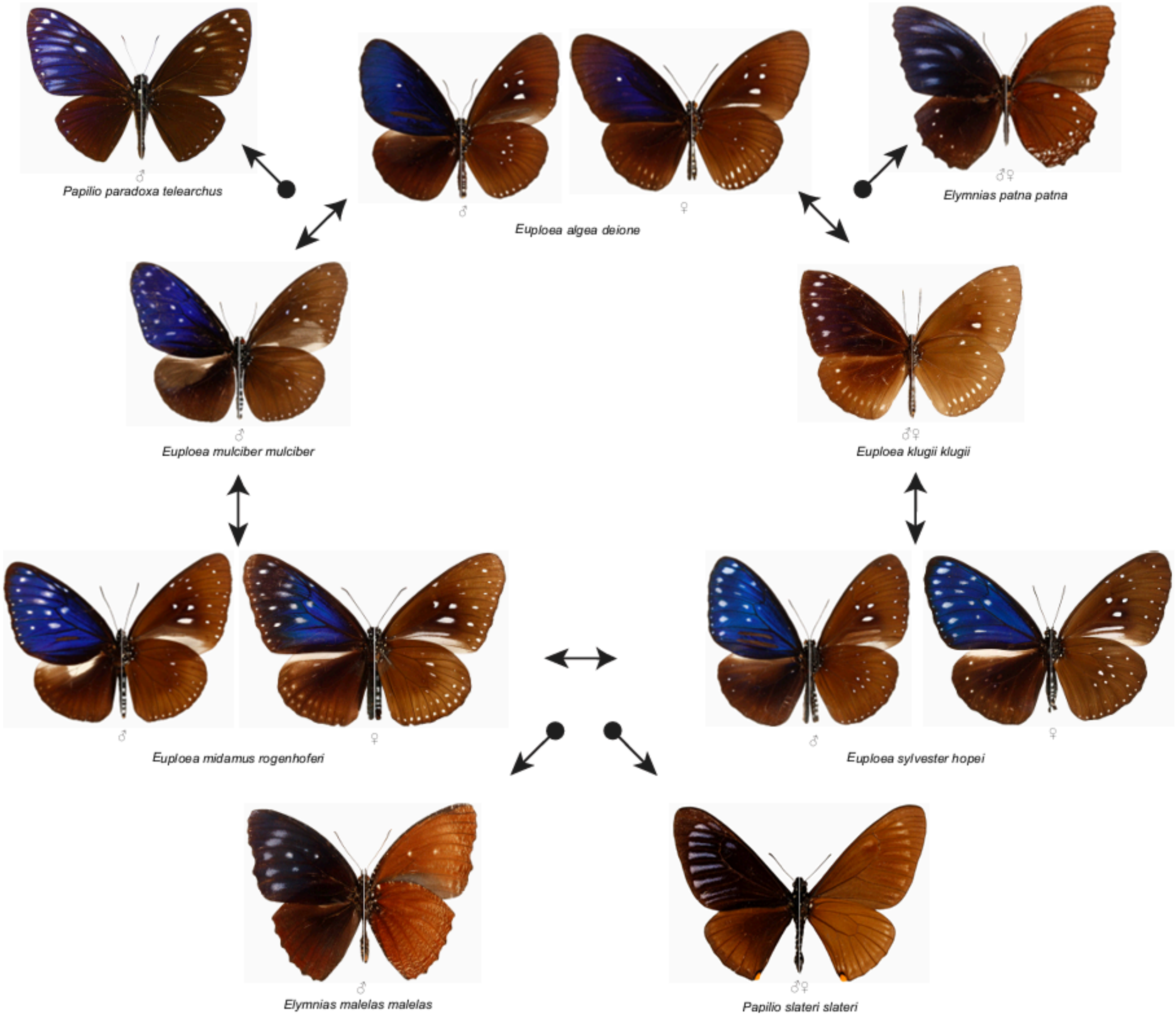


Figure 2: The Euploea blue mimicry ring with the models and mimics. The left and right sides of the wing represent the dorsal and ventral sides of the butterfly.

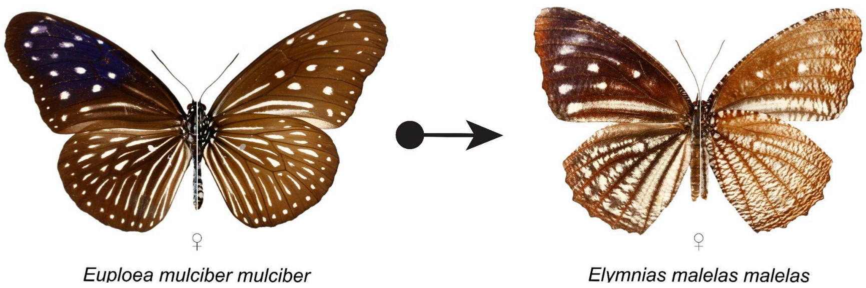
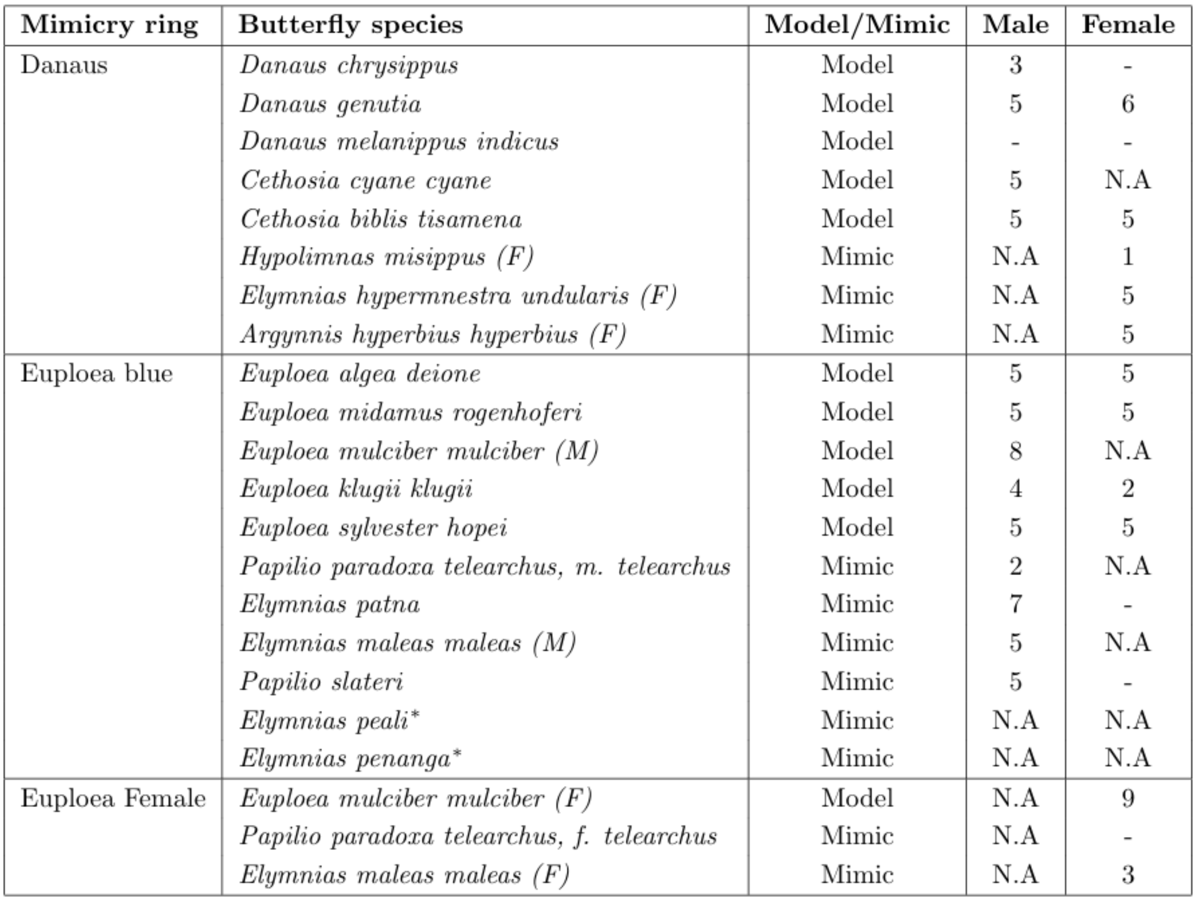


Figure 3: The Euploea female mimicry ring with the models and mimics. The left and right sides of the wing represent the dorsal and ventral sides of the butterfly.



Mimicry ring	Butterfly species	Model/Mimic	Male	Female
Danaus	*Danaus chrysippus*	Model	3	-
	Danaus genutia	Model	5	6
	Danaus melanippus indicus	Model	-	-
	Cethosia cyane cyane	Model	5	N.A
	Cethosia biblis tisamena	Model	5	5
	Hypolimnas misippus (F)	Mimic	N.A	1
	Elymnias hypermnestra undularis (F)	Mimic	N.A	5
	Argynnis hyperbius hyperbius (F)	Mimic	N.A	5
Euploea blue	*Euploea algea deione*	Model	5	5
	Euploea midamus rogenhoferi	Model	5	5
	Euploea mulciber mulciber (M)	Model	8	N.A
	Euploea klugii klugii	Model	4	2
	Euploea sylvester hopei	Model	5	5
	Papilio paradoxa telearchus, m. telearchus	Mimic	2	N.A
	Elymnias patna	Mimic	7	-
	Elymnias maleas maleas (M)	Mimic	5	N.A
	Papilio slateri	Mimic	5	-
	*Elymnias peali**	Mimic	N.A	N.A
	*Elymnias penanga**	Mimic	N.A	N.A
Euploea Female	*Euploea mulciber mulciber (F)*	Model	N.A	9
	Papilio paradoxa telearchus, f. telearchus	Mimic	N.A	-
	Elymnias maleas maleas (F)	Mimic	N.A	3

Table 1: Number of specimens measured for each butterfly species (‘N.A’: not applicable in case of male and female-limited mimicry, ‘(F)’: female-limited mimetic species, ‘(M)’: male limited-mimetic species, ‘-’ = specimen not available, ‘*’: Schedule 1 species are legally protected hence could not be accounted)

2.2 Spectral Reflectance Measurements:

The reflectance spectra of the wings were measured using an Ocean Optics Jaz spectrometer with a pulsed Xenon lamp (PX-1 lamp), which provided the illumination.

Two optical fibres outfitted with a collimating lens were used. The illuminating fibre is positioned 90 degrees to the wing surface, producing a small light spot, and the collector fibre is set at 45 degrees. The illuminating spot was approximately 1mm in diameter, smaller than the colour patch's size.

The optical fibres were aligned in the same place, both perpendicular to the butterfly wing's surface. The reflectance measured was standardised with white standard

Spectralon (Ocean Optics), which reflects >96% of the incident light, and with dark standard, where no light was allowed to reach the collecting fibre. The reflectance spectra were gathered using SpectraSuite software (OceanOptics).

All the specimens used were pinned with wings spread out flat in the same plane as the body. Specimens in good condition with little to no fading of colour or wear tear in the wings were chosen. Wherever possible, recently collected specimens were measured.

The specimens were kept on a stage level with the table to ensure the wings were parallel to the stage. The whole setup was enclosed in a box covered with a black felt cloth to exclude any kind of residual light from the room.

The reflectance of the colour patches from the forewing and hindwing of the dorsal and the ventral sides were measured. Around one to four readings of each colour patch were taken and then averaged using the R package Pavo (Maia et al., 2013).

For each colour patch, each individual's average reflectance value was used between 300 and 700 nm.

2.3 Avian Visual modelling:

Avian species usually possess tetrachromatic vision, enabling them to perceive a broad spectrum of colours. Their colour vision is mediated by four types of cone photoreceptors: long-wavelength sensitive(LWS), medium wavelength sensitive(MWS), short-wavelength sensitive(SWS), and ultraviolet sensitive(UVS) or violet sensitive(VS) (Hart & Hunt, 2007). The peak sensitivities of the LWS, MWS and SWS photoreceptors are highly conserved across the avian taxa. The species with UVS cones can perceive UV light, and the spectral sensitivity peaks near 370nm, while the ones with VS cones have peak spectral sensitivity in the violet range near 410nm and lack UV perception (Hart, 2001). Therefore, avian vision is categorised as UVS or VS and incorporating both provides us with a comprehensive understanding of how different avian species might perceive colours.

2.4 Receptor noise model:

To estimate and understand how colours are perceived and discriminated from an avian visual system, a Receptor noise model was used (Vorobyev et al., 2001, p. 2001; Vorobyev & Osorio, 1998)

The model calculates quantum catch Q_i for each cone type i as a function of photoreceptor spectral sensitivity (S_i), the reflectance spectrum of the patch (R) and the irradiance spectrum incident on the patch (I) over the visible spectrum (300-700nm):

$$Q_i = \int_{300}^{700} S_i(\lambda)R(\lambda)I(\lambda)d\lambda$$

Fechner’s law states that the receptor signal fi of cone type i is proportional to the logarithm of the quantum catch (Q_i). Hence, the difference in receptor signal Δf_i between two colours, A and B, is given by:

$$\Delta f_i = ln\frac{Q_{iA}}{Q_{iB}}$$

To account for the receptor noise of each cone, Weber fraction(ω_i) is calculated from the noise-to-signal ratio of a single receptor cone i (ν_i) and the relative number of each receptor type (n_i):

$$\omega_i = \frac{\nu_i}{\sqrt{n_i}}$$

Colour distances are then calculated by weighting the Euclidean distance of the photoreceptor quantum catches by the Weber fraction of the cones (ΔS). Since birds are tetrachromats, the equation used is as follows:

$$\Delta S = \sqrt{\frac{(\omega_1\omega_2)^2(\Delta f_4-\Delta f_3)^2+(\omega_1\omega_3)^2(\Delta f_4-\Delta f_2)^2+(\omega_1\omega_4)^2(\Delta f_3-\Delta f_2)^2+(\omega_2\omega_3)^2(\Delta f_4-\Delta f_1)^2+(\omega_2\omega_4)(\Delta f_3-\Delta f_1)^2+(\omega_3\omega_4)^2(\Delta f_2-\Delta f_1)^2}{(\omega_1\omega_2\omega_3)^2+(\omega_1\omega_2\omega_4)^2+(\omega_1\omega_3\omega_4)^2+(\omega_2\omega_3\omega_4)^2}}$$

The colour distance ΔS describes the extent of difference between two spectra. They are often quantified in the unit of JNDs (Just noticeable differences). The higher this value, the more distinguishable the two colour patches are from each other.

UVS and UV visual system's average spectral sensitivities were used to model for the avian visual perspective (Endler & Mielke, 2005b). The visual system of blue tit (*Cyanistes caeruleus*) has been extensively studied, including spectral sensitivities, cone proportions, and photoreceptor noise levels. Hence, it was used to calculate the receptor noise (1:1.92:2.68:2.7 for SWS1:SWS2:MWS: LWS cones; Hart et al., 2000). Standard daylight ("D65") was used as the irradiance spectrum, and a Weber fraction of 0.05 was used since it is the most abundant type of receptor (Delhey et al., 2015; Langmore et al., 2011; Siddiqi et al., 2004; Stoddard & Stevens, 2011).

All the modelling and the calculation were done using Pavo an R package (Maia et al., 2019)

2.5 Relative discriminability:

To determine how distinguishable a mimic is from its model compared to how much natural variation is present among the individuals of model species, relative discriminability (D_{mimic}) was computed (H˚astad et al., 2005). For every model mimic pair, the average interspecific colour distance (ΔS_c) and the average intraspecific colour distance within the model conspecific (ΔS_d) were calculated. Relative discriminability, hence, is a ratio that compares the JND between the model and mimic to the natural variation within model species and is given as follows:

$$D_{mimic} = \frac{\Delta S_c - \Delta S_d}{\sqrt{\Delta S_d}}$$

The lower the value of $D_{mimic,}$ the more the mimics resemble the model.

2.6 Statistical analyses:

The D_{mimic} values of the ventral and the dorsal side and the effect under the UVS and VS vision model for each model-mimic pair were compared, and their statistical significance was calculated using the Wilcoxon signed-rank tests and Wilcoxon rank-sum tests since the values were not normally distributed (Shapiro-Wilk test). All the statistical analysis and the pairwise comparison were performed in R (*R Core Team; R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing,* 2023).

Chapter 3 Results

Box plots were plotted to see how the colours from the dorsal and the ventral side of the butterfly wing were being perceived according to the avian visual perspective. Plots for both UVS and VS birds were plotted. Each mimic was compared with each model, and the values of D_{mimic} and the Wilcoxon signed-rank tests and Wilcoxon rank-sum tests analytics results for all the comparisons were tabulated. In all the figures, the sex mentioned in the legend represents the model sex.

3.1 Danaus Mimicry Ring

The D_{mimic} values of each model mimic pair, the values after the Wilcoxon signed-rank test for the comparison under different visual models and the Wilcoxon rank-sum test for the comparing the two surfaces have been tabulated.

The D_{mimic} values of the dorsal and the ventral side of each pair were compared under the two avian vision models (UVS and VS) and plotted.

Model	Mimic	Wing Side	UVS		VS	
			Male Dmimic (Mean± SD)	Female Dmimic (Mean± SD)	Male Dmimic (Mean± SD)	Female Dmimic (Mean± SD)
Danaus chrysippus	*Elymnias hypermnestra undularis* (F)	Dorsal	0.19±1.11	-	0.21±1.33	-
		Ventral	0.51±0.71	-	0.39±0.62	-
	Argynnis hyperbius hyperbius (F)	Dorsal	0.44±1.07	-	0.50±1.20	-
		Ventral	0.46±0.90	-	0.14±0.95	-
Danaus genutia	*Elymnias hypermnestra undularis* (F)	Dorsal	1.08±1.39	0.62±0.82	1.91±1.88	1.14±1.31
		Ventral	1.11±1.43	0.64±0.98	1.83±1.86	1.16±1.25
	Argynnis hyperbius hyperbius (F)	Dorsal	2.08±1.66	1.24±1.23	2.08±1.73	1.24±1.28
		Ventral	1.41±1.58	1.12±1.11	1.03±1.30	0.86±0.92
Cethosia cyane cyane (M)	*Elymnias hypermnestra undularis* (F)	Dorsal	1.55±1.94	-	1.15±1.27	-
		Ventral	0.68±0.80	-	0.36±0.51	-
	Argynnis hyperbius hyperbius (F)	Dorsal	1.89±2.36	-	1.29±1.56	-
		Ventral	0.33±1.48	-	0.33±1.15	-
Cethosia biblis tisamena	*Elymnias hypermnestra undularis* (F)	Dorsal	4.12±5.49	0.64±1.24	3.75±5.26	0.39±1.01
		Ventral	2.31±0.90	0.54±0.54	2.79±1.27	0.66±0.90
	Argynnis hyperbius hyperbius (F)	Dorsal	4.53±5.84	-0.05±0.61	4.08±5.66	-0.21±0.22
		Ventral	2.39±2.27	0.69±1.00	2.74±2.66	0.79±1.06

Table 2: Relative discriminability (D_{mimic}) values for Danaus mimicry ring. The last four columns mention the model sex compared to the mimic.

Model	**Model Sex**	**Wing Side**	**Mimic**			
			Elymnias hypermnestra undularis (F)		*Argynnis hyperbius hyperbius* (F)	
			p-value	**V**	**p-value**	**V**
*Danaus chrysippus**	*Male*	Dorsal	0.8125	6	0.4365	4
		Ventral	0.5	5	0.0625	20
Danaus genutia	*Male*	Dorsal	1	10	1	11
		Ventral	0.75	4	0.4375	15
	Female	Dorsal	1	10	0.1563	18
		Ventral	0.75	2	0.937	19
Cethosia cyane cyane (M)	*Male*	Dorsal	0.5	5	0.3125	12
		Ventral	0.7	6	0.8438	9
Cethosia biblis tisamena	*Male*	Dorsal	0.1875	13	0.0625	15
		Ventral	0.25	0	0.2188	4
	Female	Dorsal	0.3125	12	1	8
		Ventral	1	3	0.4375	6

Table 3: Wilcoxon signed-rank test values for comparison of wing side perception under UVS and VS vision model in the Danaus mimicry ring. *Both males and females of these species participate in the mimicry ring, but only the sex with a sufficient number of specimens was included in the analysis.

Model	**Model Sex**	**Wing Side**	**Mimic**			
			Elymnias hypermnestra undularis (F)		*Argynnis hyperbius hyperbius* (F)	
			p-value	**W**	**p-value**	**W**
*Danaus chrysippus**	*Male*	UVS	0.393	4	0.931	14
		VS	0.25	3	0.931	16
Danaus genutia	*Male*	UVS	0.262	4	0.485	23
		VS	0.381	5	0.309	25
	Female	UVS	0.548	6	1	18
		VS	0.381	5	0.699	21
Cethosia cyane cyane (M)	*Male*	UVS	0.786	9	0.177	23
		VS	0.786	9	0.429	20
Cethosia biblis tisamena	*Male*	UVS	0.786	6	0.931	16
		VS	0.786	6	1	15
	Female	UVS	1	7	1.77	7
		VS	0.786	6	0.03	3

Table 4: Wilcoxon rank-sum test values for comparison of dorsal and ventral sides under a fixed vision model in the Danaus mimicry ring. *Both males and females of these species participate in the mimicry ring, but only the sex with a sufficient number of specimens was included in the analysis.

1. *Danaus chrysippus* (M) - *Elymnias hypermnestra undularis* (F)

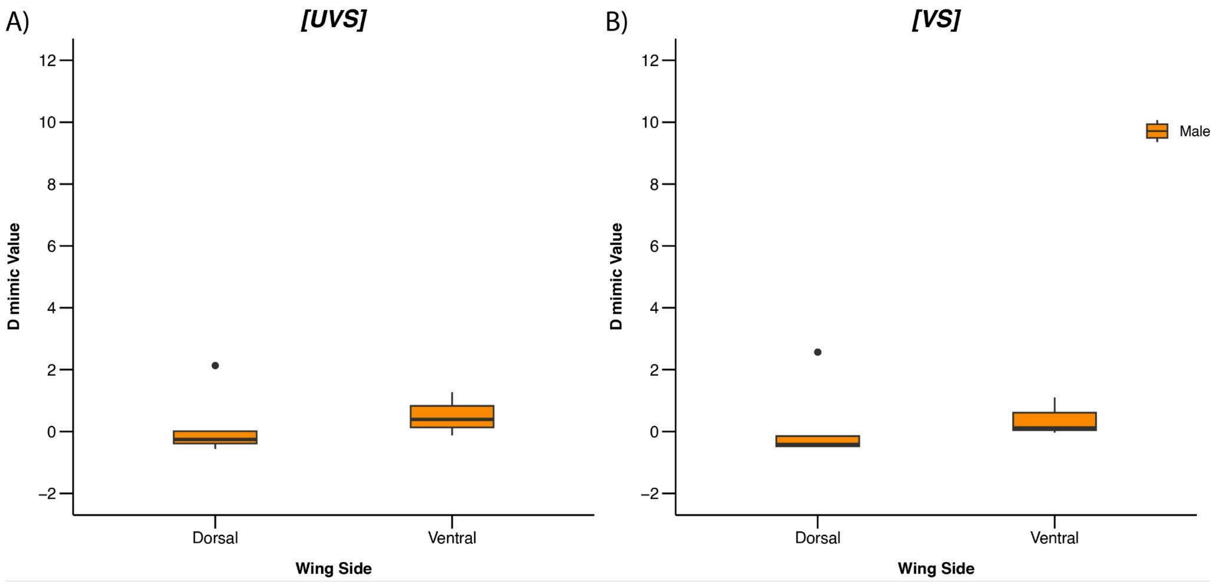


Figure 4: Relative discriminability (D_{mimic}) between the model *Danaus chrysippus* (Male) and mimic *Elymnias hypermnestra undularis* (Female) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 4), the dorsal side had lower D_{mimic} values than the ventral side. Between the two vision models, the VS has lower D_{mimic} value than UVS. However, the statistical tests indicated that the differences in both cases were not statistically significant.

2. *Danaus genutia* (M&F) - *Elymnias hypermnestra undularis* (F)

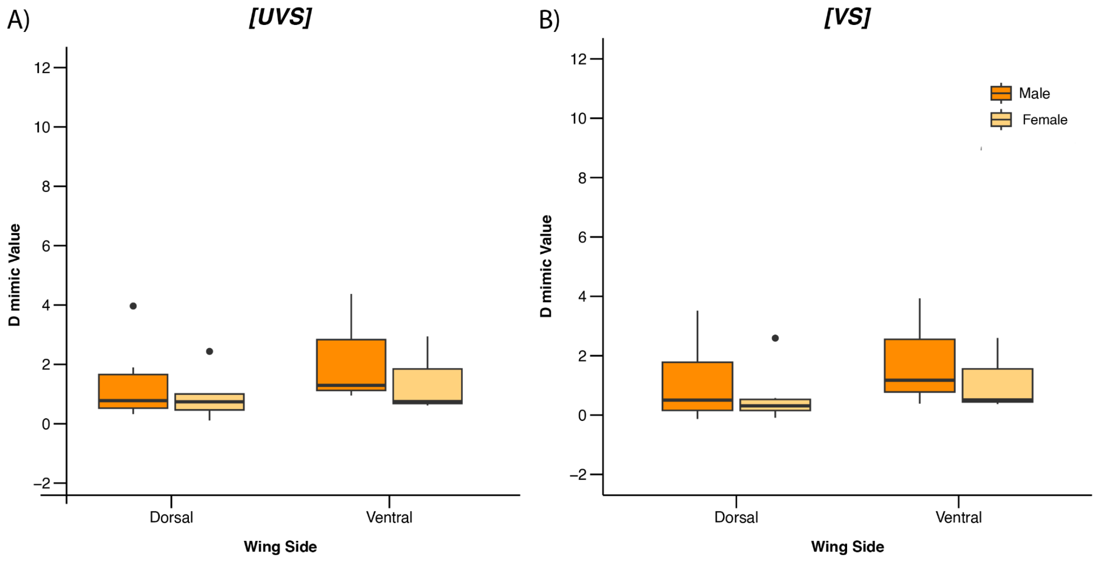


Figure 5: Relative discriminability (D_{mimic}) between the model *Danaus genutia* (Male & Female) and mimic *Elymnias hypermnestra undularis* (Female) using avian (A) UVS and (B) VS visual system.

Under both vision models (Figure 5), the dorsal side had lower D_{mimic} values than the ventral side. Between the two vision models, the UVS has lower D_{mimic} values than the VS visual system. However, the statistical tests indicated that the differences in both cases were not statistically significant. The comparison of the mimic to the female model overall had lower values as compared to the male models.

3. *Cethosia cyane cyane* (M) - *Elymnias hypermnestra undularis* (F)

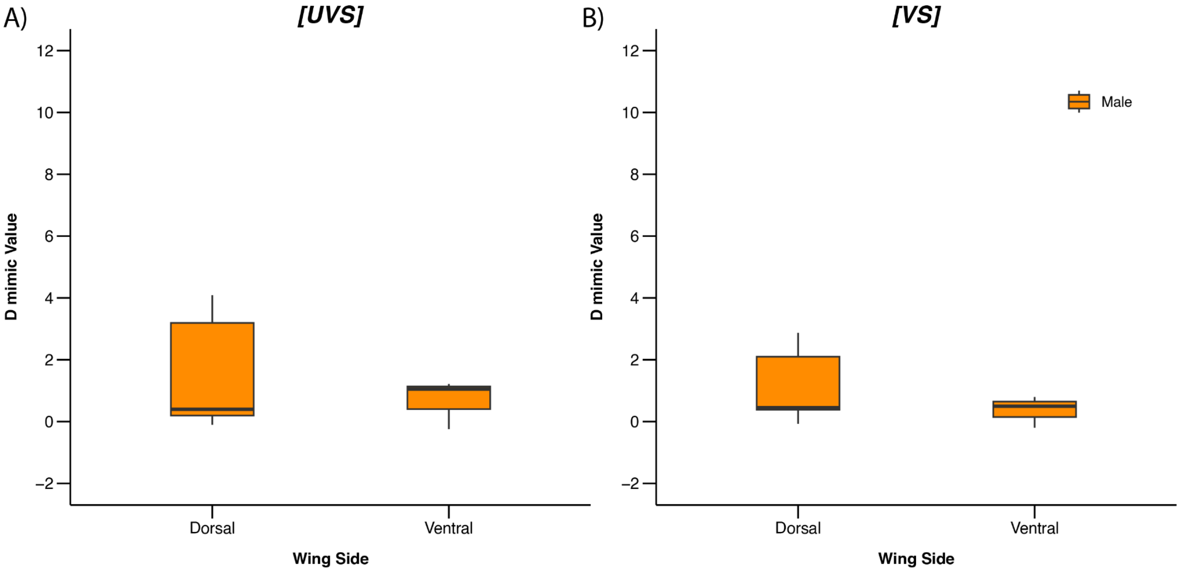


Figure 6: Relative discriminability (D_{mimic}) between the model *Cethosia cyane cyane* (Male) and mimic *Elymnias hypermnestra undularis* (Female) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 6), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the VS has lower D_{mimic} values than the UVS visual system. However, the statistical tests indicated that the differences in both cases were not statistically significant.

4. *Cethosia biblis tisamena* (M&F) - *Elymnias hypermnestra undularis* (F)

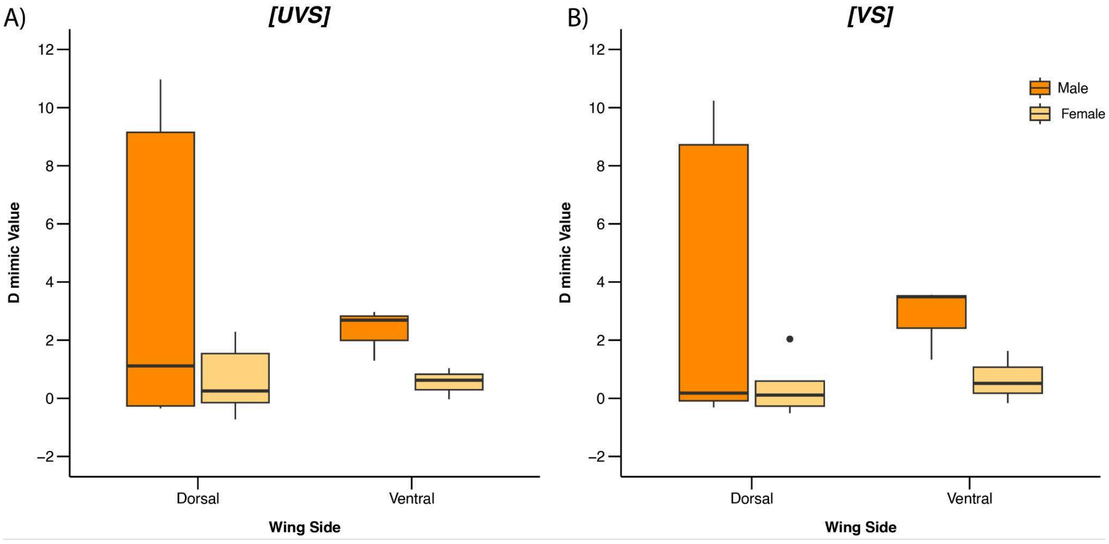


Figure 7: Relative discriminability (D_{mimic}) between the model *Cethosia biblis tisamena* (Male & Female) and mimic *Elymnias hypermnestra undularis* (Female) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 7), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, UVS has a lower D_{mimic} value for the ventral side, whereas VS has a lower D_{mimic} value for the dorsal side. However, the statistical tests indicated that the differences in both cases were not statistically significant. The comparison of the mimic to the female model overall had lower values as compared to the male models.

5. *Danaus chrysippus* (M) - *Argynnis hyperbius hyperbius* (F)

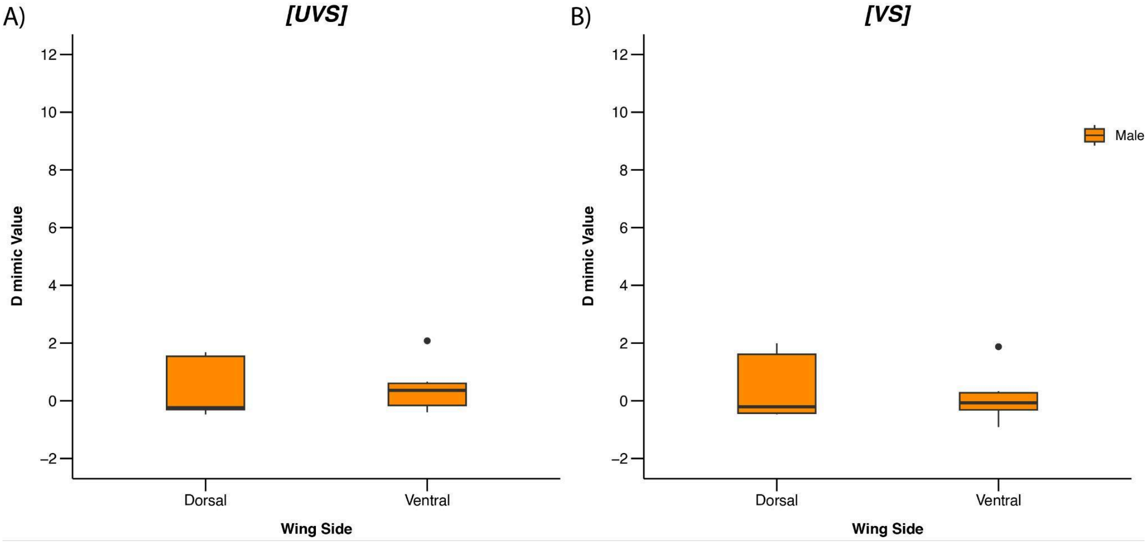


Figure 8: Relative discriminability (D_{mimic}) between the model *Danaus chrysippus* (Male) and mimic *Argynnis hyperbius hyperbius* (Female) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 8), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the VS has lower D_{mimic} values than the UVS visual system for the ventral side, but opposite for the dorsal side. However, the statistical tests indicated that the differences in both cases were not statistically significant.

6. *Danaus genutia* (M&F) - *Argynnis hyperbius hyperbius* (F)

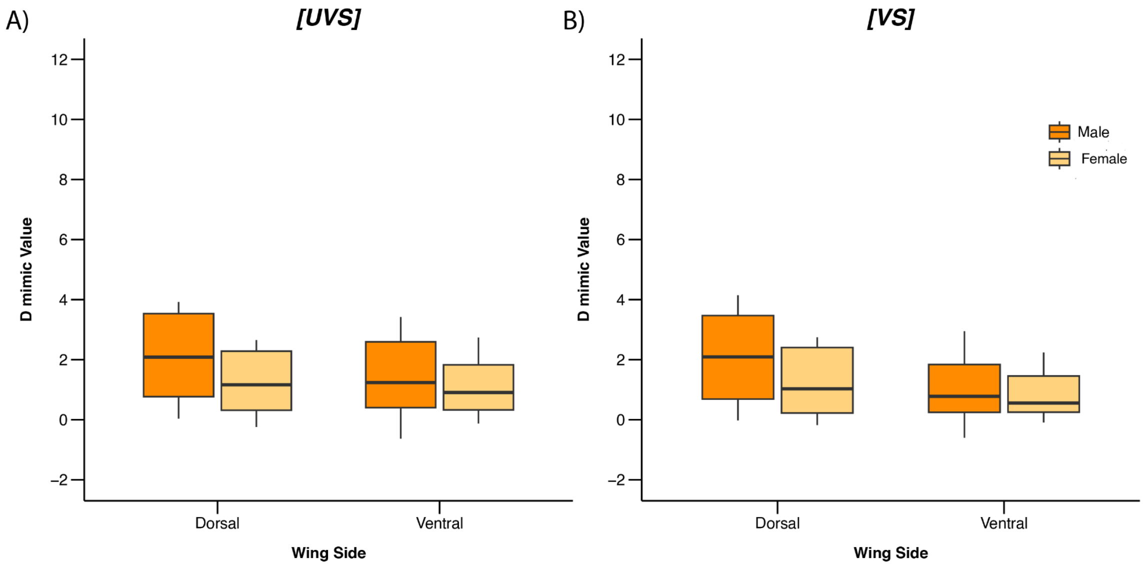


Figure 9: Relative discriminability (D_{mimic}) between the model *Danaus genutia* (Male & Female) and mimic *Argynnis hyperbius hyperbius* (Female) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 9), the ventral side had lower D_{mimic} values than the dorsal side. However, the statistical tests indicated that the differences were not statistically significant. The two vision models had nearly the same D_{mimic} values. The comparison of the mimic to the female model overall had lower values as compared to the male models.

7. *Cethosia cyane cyane* (M) - *Argynnis hyperbius hyperbius* (F)

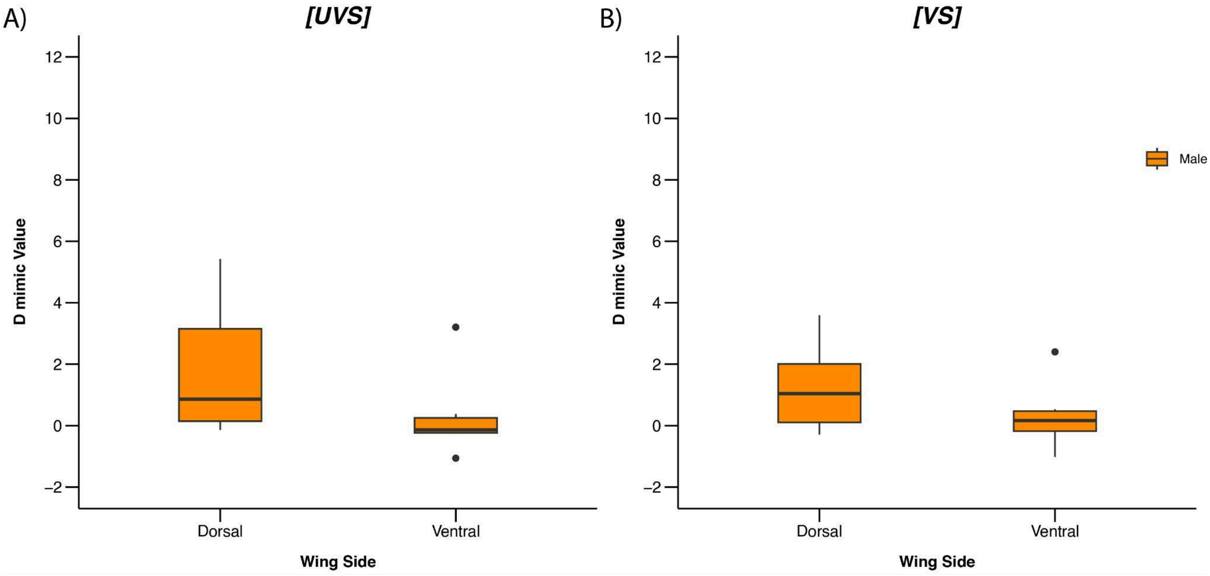


Figure 10: Relative discriminability (D_{mimic}) between the model *Cethosia cyane cyane* (Male) and mimic *Argynnis hyperbius hyperbius* (Female) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 10), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the VS has lower D_{mimic} value for the dorsal side but not significantly different and the ventral side has nearly the same values. However, the statistical tests indicated that the differences in both cases were not statistically significant.

8. *Cethosia biblis tisamena* (M&F) - *Argynnis hyperbius hyperbius* (F)

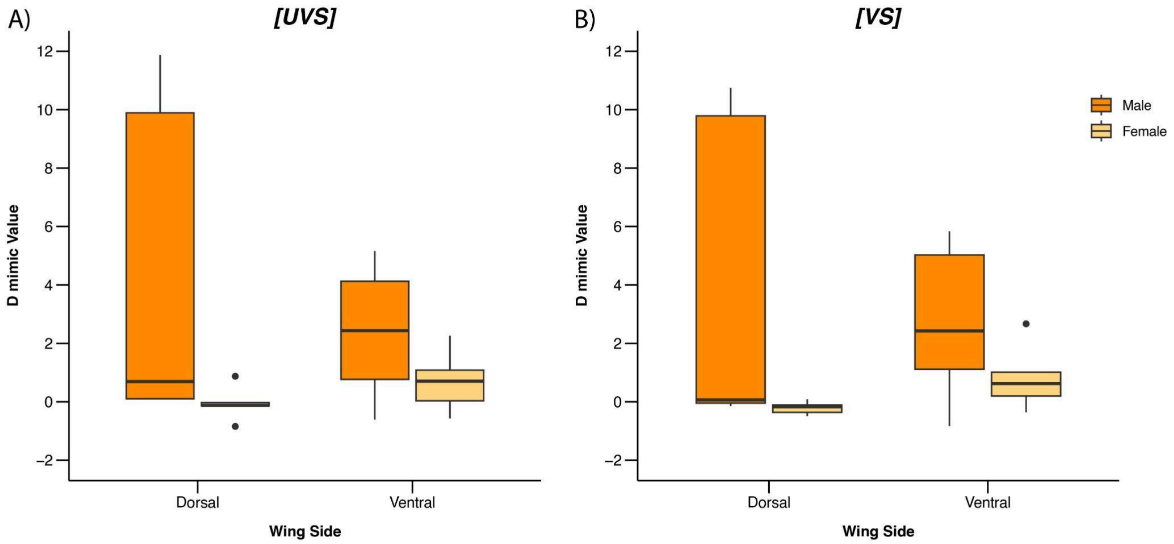


Figure 11: Relative discriminability (D_{mimic}) between the model *Cethosia biblis tisamena* (Male & Female) and mimic *Elymnias hypermnestra undularis* (Female) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 11), the comparison to the male model had lower D_{mimic} values for the ventral side. For the comparison to the female model, the dorsal side had lower values under both vision systems. Between the two vision models, the UVS has lower D_{mimic} values compared to VS. However, the statistical tests indicated that the differences in both cases were not statistically significant. The comparison of the mimic to the female model overall had lower values as compared to the male models.

Summary: Danaus Mimicry Ring

The model mimic pairs in this ring had generally lower D_{mimic} value for the ventral wing surface as compared to the dorsal side under both UVS and VS visual model systems. Although there were slight differences between vision models, such as lower D_{mimic} value under UVS for some pairs and under VS for some pairs, none of these differences were statistically significant. Comparisons involving both male and female models reveal that the mimic tended to resemble the female model closely than their male counterparts, but again these differences were not statistically significant.

3.2 Euploea Blue Mimicry Ring

The D_{mimic} values of each model mimic pair, the values after the Wilcoxon signed-rank test for the comparison under different visual models and the Wilcoxon rank-sum test for comparing the two surfaces have been tabulated.

The D_{mimic} values of the dorsal and the ventral side of each pair were compared under the two avian vision models (UVS and VS) and plotted.

Model	Mimic	Wing Side	UVS		VS	
			Male Dmimic (Mean± SD)	Female Dmimic (Mean± SD)	Male Dmimic (Mean± SD)	Female Dmimic (Mean± SD)
Euploea algea deione	*Elymnias patna*	Dorsal	2.80±3.57	2.54±1.37	2.47±3.46	2.15±1.92
		Ventral	-0.45±0.21	-0.28±0.41	-0.46±0.21	-0.36±0.29
	Elymnias malelas malelas (M)	Dorsal	1.74±2.87	0.97±1.82	1.56±2.85	0.93±2.02
		Ventral	0.63±1.99	0.63±1.68	0.62±1.96	0.61±1.73
	Papilio slateri	Dorsal	2.32±2.59	0.59±2.00	1.75±2.38	0.50±1.81
		Ventral	-0.50±0.26	-0.40±0.15	-0.50±0.15	-0.43±0.19
Euploea midamus rogenhoferi	*Elymnias patna*	Dorsal	1.64±1.24	4.27±2.67	1.41±0.92	4.71±2.74
		Ventral	-0.31±0.28	0.90±0.50	-0.08±0.25	0.50±0.42
	Elymnias malelas malelas (M)	Dorsal	0.71±2.45	0.09±0.61	1.76±2.97	2.93±1.97
		Ventral	0.72±1.61	1.22±1.00	0.92±1.49	1.40±1.03
	Papilio slateri	Dorsal	0.34±0.96	1.69±2.23	0.13±0.62	1.89±2.35
		Ventral	-0.32±0.10	0.05±0.41	-0.29±0.18	-0.27±0.43
Euploea mulciber mulciber (M)	*Elymnias patna*	Dorsal	1.53±1.66	-	1.34±1.57	-
		Ventral	0.13±0.51	-	0.12±0.22	-
	Elymnias malelas malelas (M)	Dorsal	0.71±1.56	-	0.09±0.61	-
		Ventral	0.24±0.22	-	0.10±0.21	-
	Papilio slateri	Dorsal	0.57±1.10	-	0.23±0.78	-
		Ventral	-0.16±0.24	-	-0.34±0.09	-
Euploea klugii klugii	*Elymnias patna*	Dorsal	3.66±1.25	-	3.57±1.66	-
		Ventral	0.23±0.77	-	0.62±1.11	-
	Elymnias malelas malelas (M)	Dorsal	2.33±2.08	-	2.40±2.53	-
		Ventral	0.21±0.46	-	0.25±0.34	-
	Papilio slateri	Dorsal	1.06±1.77	-	0.47±1.92	-
		Ventral	-0.45±0.31	-	-0.36±0.14	-
Euploea sylvester hopei	*Elymnias patna*	Dorsal	1.89±2.08	1.19±2.49	1.50±1.53	0.98±2.16
		Ventral	0.01±0.59	-0.90±0.90	0.01±0.49	0.80±0.76
	Elymnias malelas malelas (M)	Dorsal	0.70±0.82	-0.05±0.60	0.54±0.86	-0.01±0.50
		Ventral	0.86±1.00	2.64±0.78	0.81±0.91	2.29±0.60
	Papilio slateri	Dorsal	2.80±3.57	2.54±1.37	2.47±3.46	2.15±1.92
		Ventral	-0.45±0.21	-0.28±0.41	-0.46±0.21	-0.36±0.29

Table 5: Relative discriminability (D_{mimic}) values for Euploea blue mimicry ring. The last four columns mention the model sex compared to the mimic.

Model	**Model Sex**	**Wing Side**	**Mimic**					
			*Elymnias patna**		*Elymnias malelas malelas (M)*		*Papilio slateri**	
			p-value	**V**	**p-value**	**V**	**p-value**	**V**
Euploea algea deione	*Male*	Dorsal	0.25	6	0.25	6	0.25	6
		Ventral	0.875	6	1	3	1	1
	Female	Dorsal	0.5	3	1	2	1	2
		Ventral	0.875	6	1	3	0.5	3
Euploea midamus rogenhoferi	*Male*	Dorsal	0.5	5	0.5	1	0.5	5
		Ventral	0.25	1	0.25	0	1	1
	Female	Dorsal	0.75	2	0.5	1	0.25	0
		Ventral	0.125	0	0.25	0	0.5	0
Euploea mulciber mulciber (M)	*Male*	Dorsal	1	3	0.5	5	0.5	3
		Ventral	0.875	4	0.5	3	1	2
*Euploea klugii klugii**	*Male*	Dorsal	0.875	4	0.75	2	0.25	6
		Ventral	0.25	1	1	3	1	1
Euploea sylvester hopei	*Male*	Dorsal	0.5	5	0.25	6	0.75	4
		Ventral	1	5	0.25	6	1	1
	Female	Dorsal	0.5	5	0.75	2	0.5	1
		Ventral	0.625	7	0.25	6	0.5	0

Table 6: Wilcoxon signed-rank test values for comparison of wing side perception under UVS and VS vision model in the Euploea blue female mimicry ring. *Both males and females of these species participate in the mimicry ring, but only the sex with a sufficient number of specimens was included in the analysis.

Model	**Model Sex**	**Wing Side**	**Mimic**					
			*Elymnias patna**		*Elymnias malelas malelas (M)*		*Papilio slateri**	
			p-value	**W**	**p-value**	**W**	**p-value**	**W**
Euploea algea deione	*Male*	UVS	0.057	12	1	5	0.4	5
		VS	0.886	12	1	5	0.8	4
	Female	UVS	0.133	8	1	3	1	2
		VS	0.057	12	0.8	2	1	2
Euploea midamus rogenhoferi	*Male*	UVS	0.057	12	0.7	6	0.8	4
		VS	0.057	12	1	5	0.8	4
	Female	UVS	0.057	12	0.4	7	0.8	4
		VS	0.057	12	0.7	6	0.8	4
Euploea mulciber mulciber (M)	*Male*	UVS	0.629	8	1	3	0.666	3
		VS	0.629	8	0.8	2	0.666	3
*Euploea klugii klugii **	*Male*	UVS	0.028	16	0.4	7	0.4	5
		VS	0.057	15	1	4	0.8	2
Euploea sylvester hopei	*Male*	UVS	0.229	10	0.7	3	0.4	5
		VS	0.229	10	0.7	3	0.8	4
	Female	UVS	0.629	4	0.1	0	0.2	0
		VS	0.629	4	0.1	0	0.2	0

Table 7: Wilcoxon rank-sum test values for comparison of dorsal and ventral sides under a fixed vision model in the Euploea blue female mimicry ring. *Both males and females of these species participate in the mimicry ring, but only the sex with a sufficient number of specimens was included in the analysis.

1. *Euploea algea deione* (M&F) - *Elymnias patna* (M)

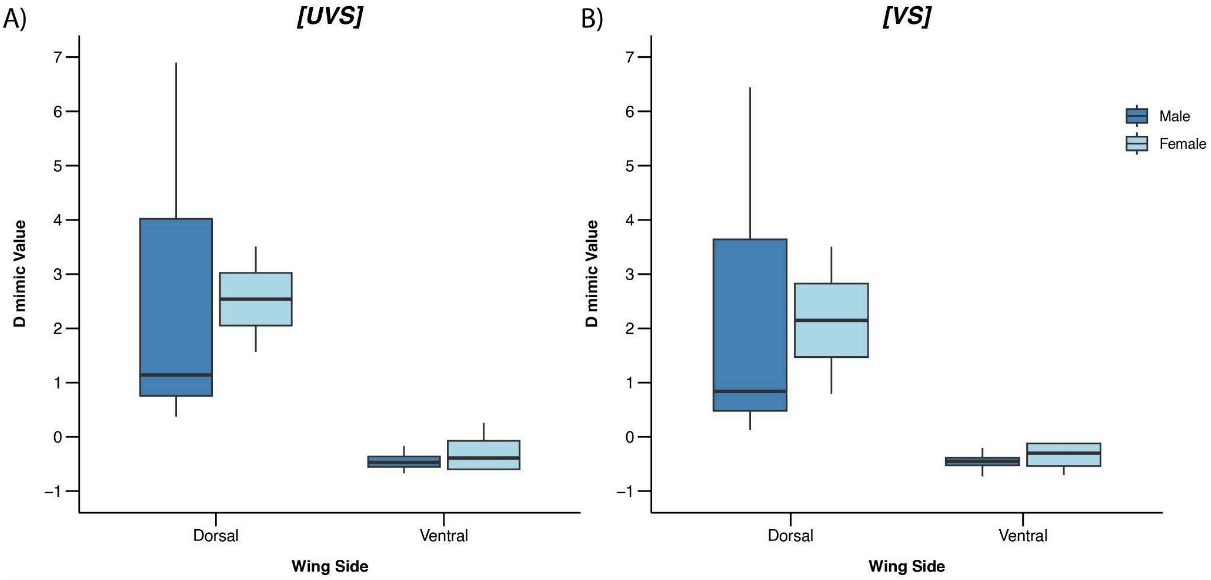


Figure 12: Relative discriminability (D_{mimic}) between the model *Euploea algea deione* (Male & Female) and the mimic *Elymnias patna* (Male)using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 12), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the VS has lower D_{mimic} values compared to UVS for the dorsal side, but the ventral side has nearly the same values. However, the statistical tests indicated that the differences in both cases were not statistically significant. The comparison of the mimic to the female model overall had lower values as compared to the male models.

2. *Euploea midamus rogenhoferi* (M&F) - *Elymnias patna* (M)

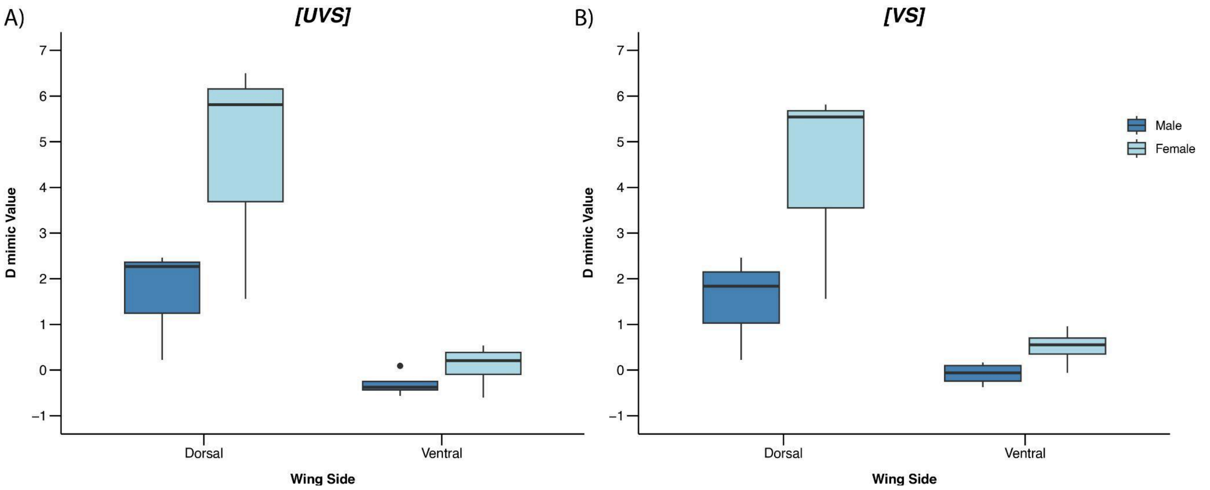


Figure 13: Relative discriminability (D_{mimic}) between the model *Euploea midamus rogenhoferi* (Male & Female) and the mimic *Elymnias patna* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 13), the ventral side had lower D_{mimic} values than the dorsal side, which were statistically significant differences. The two vision models had nearly the same D_{mimic} values for dorsal, but the VS had lower D_{mimic} values for the ventral side. However, the statistical tests indicated that the differences were not statistically significant. The comparison of the mimic to the female model overall had lower values as compared to the male models.

3. *Euploea mulciber mulciber* (M) - *Elymnias patna* (M)

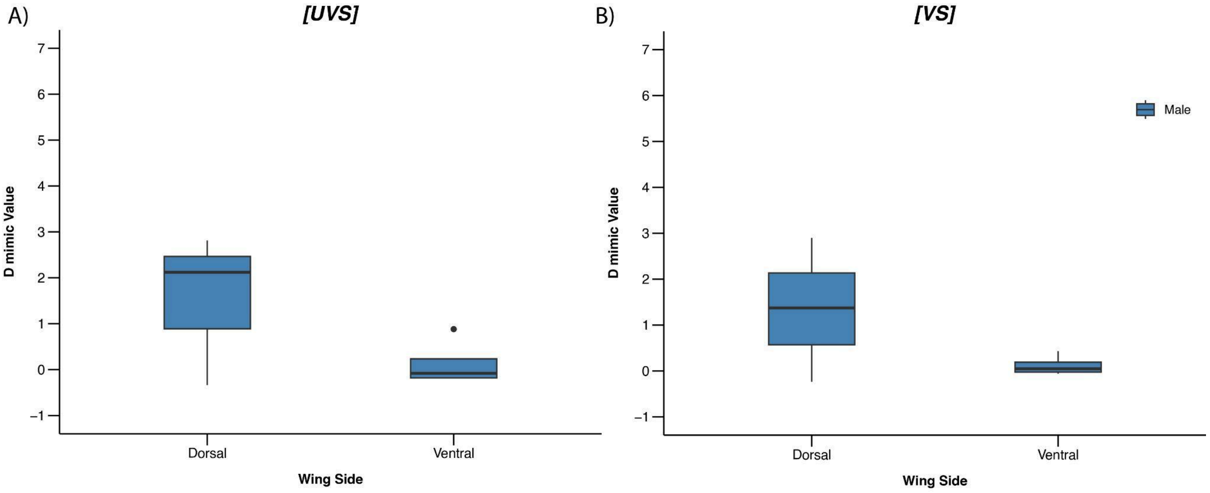


Figure 14: Relative discriminability (D_{mimic}) between the model *Euploea mulciber mulciber* (Male) and the mimic *Elymnias patna* (Male) using avian (A)UVS and (B) VS visual system

Under both vision models (Figure 14), the ventral side had lower D_{mimic} values than the dorsal side. However, the statistical tests indicated that the differences in both cases were not statistically significant. The two vision models had nearly the same D_{mimic} values.

4. *Euploea klugii klugii* (M) - *Elymnias patna* (M)

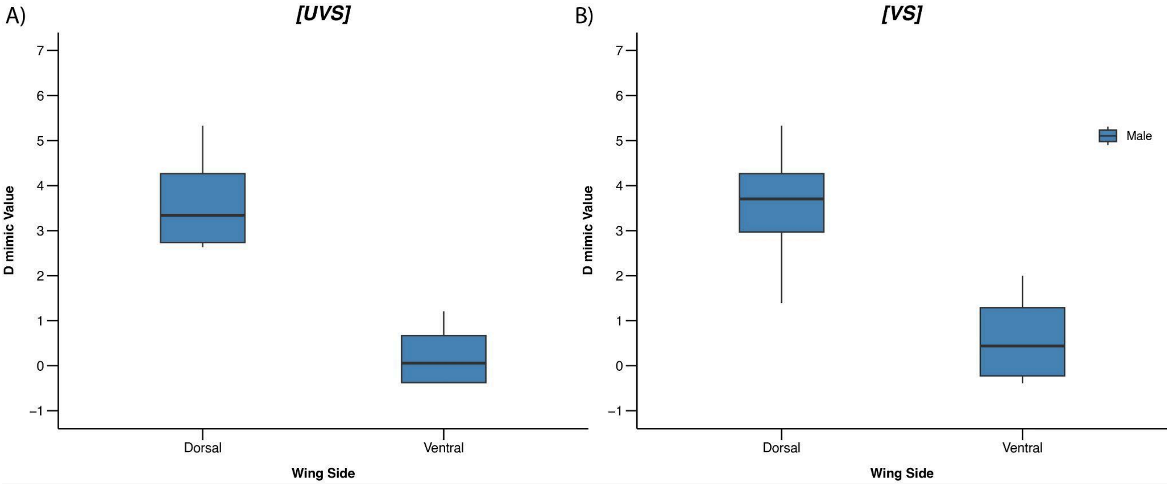


Figure 15: Relative discriminability (D_{mimic}) between the model *Euploea klugii klugii* (Male) and the mimic *Elymnias patna* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 15), the ventral side had lower D_{mimic} values than the dorsal side, which were statistically significant differences. Between the two vision models, the UVS has lower D_{mimic} values compared to VS for the ventral side, but the dorsal side has nearly the same values. However, the statistical tests indicated that the differences were not statistically significant.

5. *Euploea sylvester hopei* (M&F) - *Elymnias patna* (M)

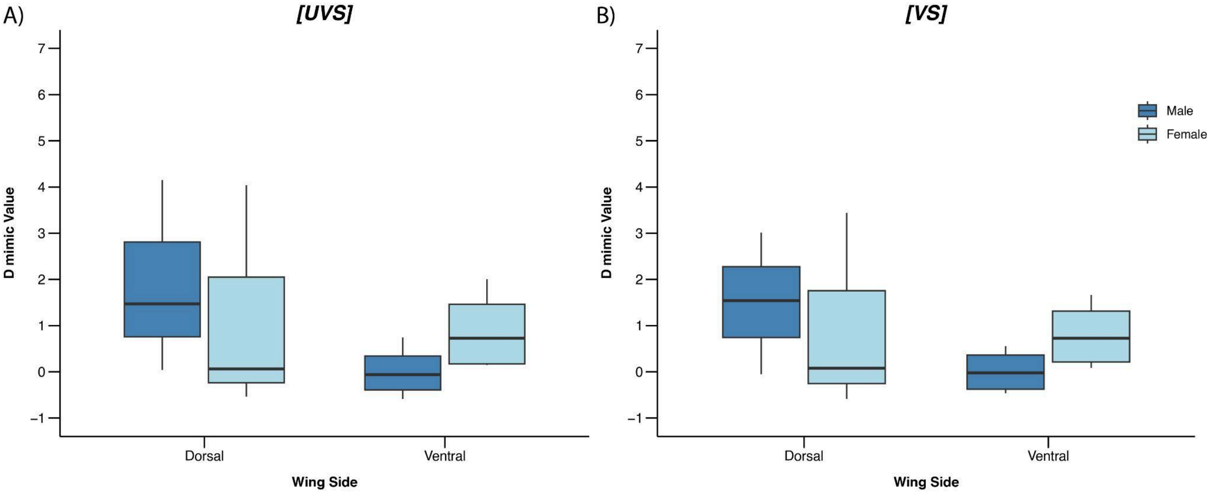


Figure 16: Relative discriminability (D_{mimic}) between the model *Euploea sylvester hopei* (Male & Female) and the mimic *Elymnias patna* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 16), the ventral side had lower D_{mimic} values than the dorsal side. However, the statistical tests indicated that the differences were not statistically significant. The two vision models had nearly the same D_{mimic} values except for the comparison of the mimic to the female model under the VS visual system. The comparison of the mimic to the female model overall had lower values as compared to the male models.

6. *Euploea algea deione* (M&F) - *Elymnias malelas malelas* (M)

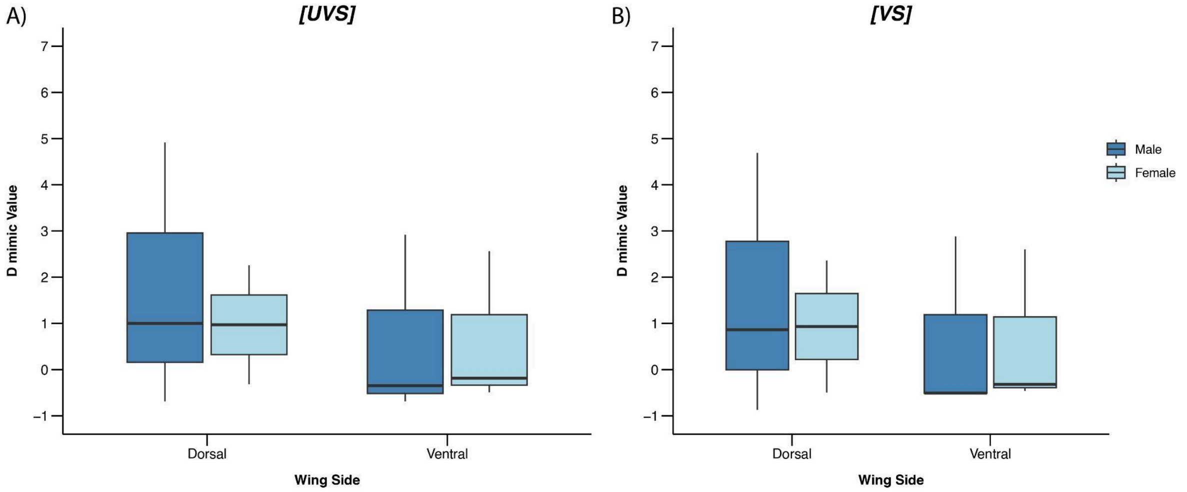


Figure 17: Relative discriminability (D_{mimic}) between the model *Euploea algea deione* (Male & Female) and the mimic *Elymnias malelas malelas* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 17), the ventral side had lower D_{mimic} values than the dorsal side. However, the statistical tests indicated that the differences were not statistically significant. The two vision models had nearly the same D_{mimic} values. The comparison of the mimic to the female model overall had lower values as compared to the male models.

7. *Euploea midamus rogenhoferi* (M&F) - *Elymnias malelas malelas* (M)

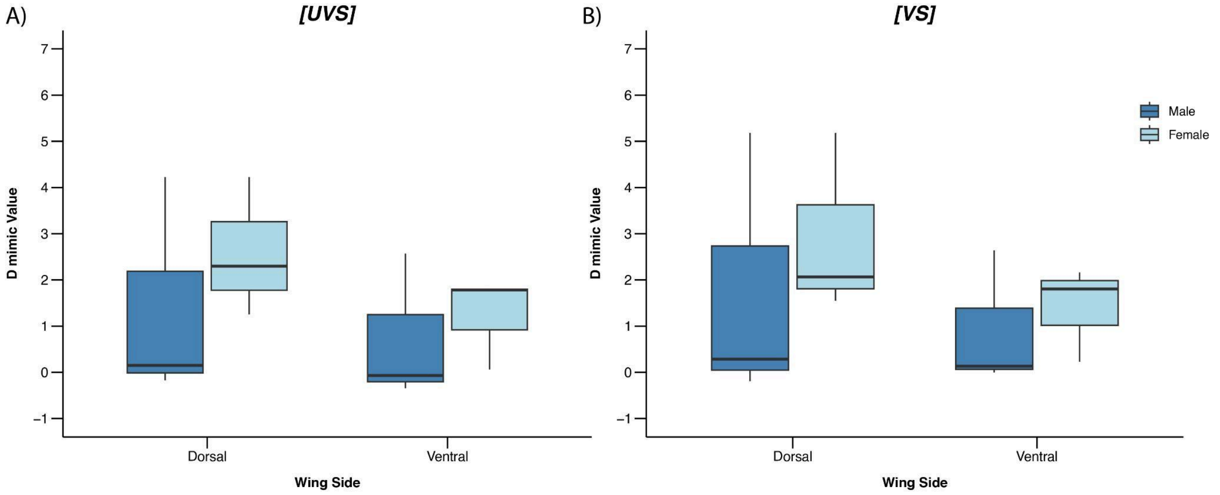


Figure 18: Relative discriminability (D_{mimic}) between the model *Euploea midamus rogenhoferi* (Male & Female) and the mimic *Elymnias malelas malelas* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 18), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the UVS has lower D_{mimic} values compared to VS. However, the statistical tests indicated that the differences were not statistically significant. The comparison of the mimic to the male model overall had lower values as compared to the female models.

8. *Euploea mulciber mulciber* (M) - *Elymnias malelas malelas* (M)

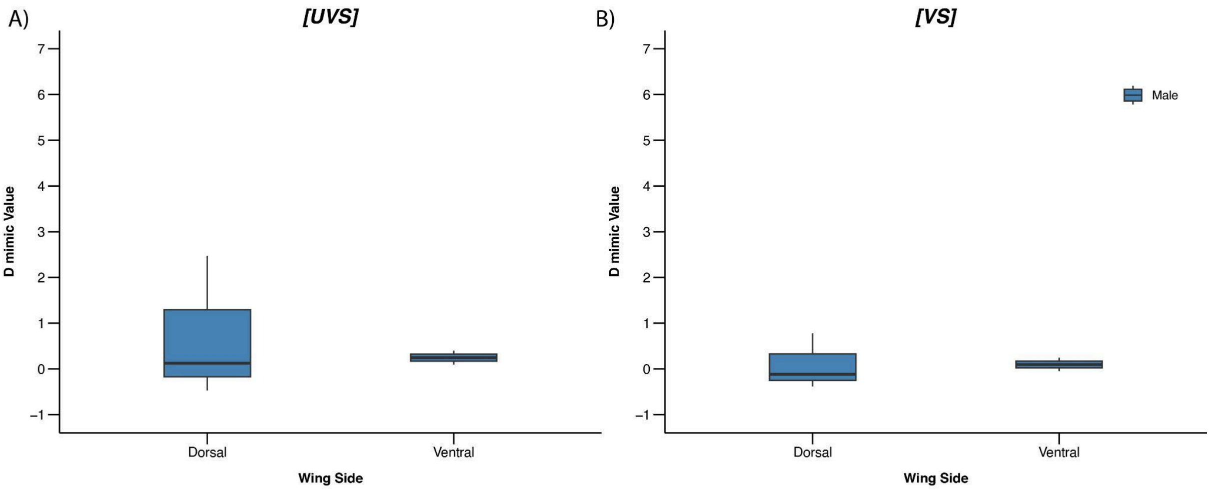


Figure 19: Relative discriminability (D_{mimic}) between the model *Euploea mulciber mulciber* (Male) and the mimic *Elymnias malelas malelas* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 19), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the VS has lower D_{mimic} values compared to UVS. However, the statistical tests indicated that the differences were not statistically significant.

9. *Euploea klugii klugii* (M) - *Elymnias malelas malelas* (M)

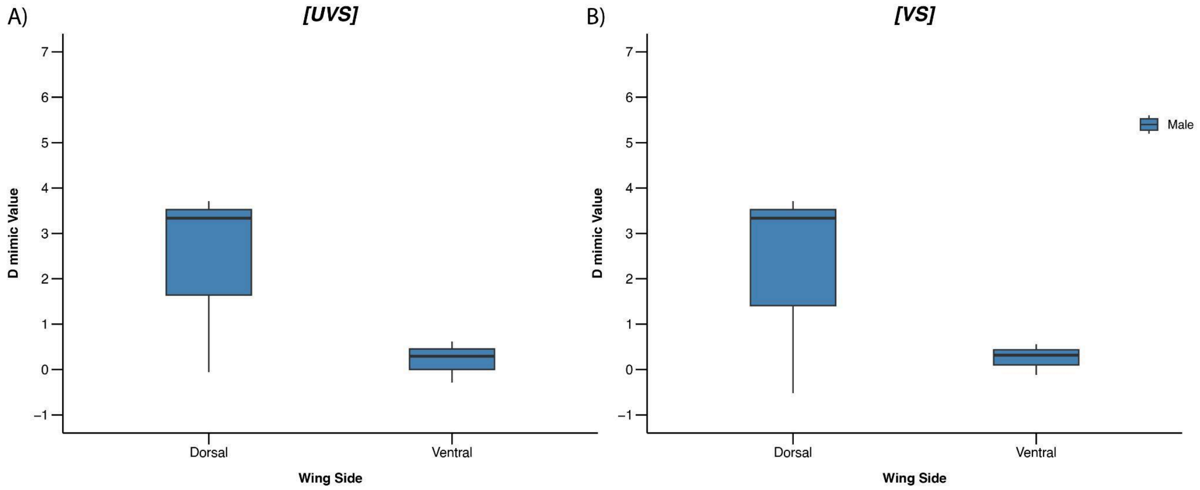


Figure 20: Relative discriminability (D_{mimic}) between the model *Euploea klugii klugii* (Male) and the mimic *Elymnias malelas malelas* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 20), the ventral side had lower D_{mimic} values than the dorsal side. However, the statistical tests indicated that the differences were not statistically significant. The two vision models had nearly the same D_{mimic} values.

10. *Euploea sylvester hopei* (M&F) - *Elymnias malelas malelas* (M)

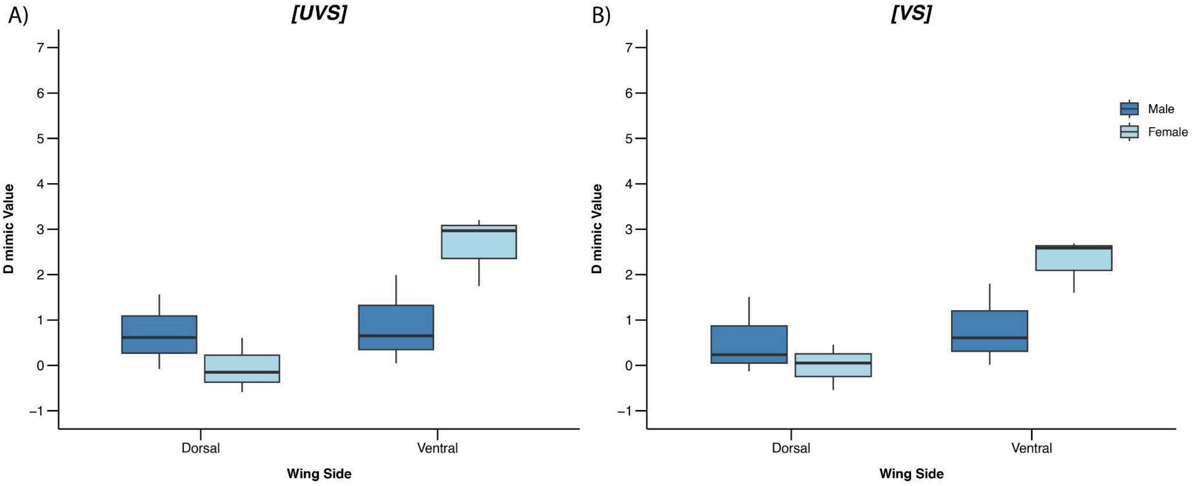


Figure 21: Relative discriminability (D_{mimic}) between the model *Euploea sylvester hopei* (Male & Female) and the mimic *Elymnias malelas malelas* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 21), the dorsal side had lower D_{mimic} values than the ventral side. Between the two vision models, the VS has lower D_{mimic} values compared to UVS for the dorsal side but nearly the same for the ventral side. However, the statistical tests indicated that the differences were not statistically significant. The comparison of the mimic to the male model had lower values as compared to the female models for the ventral but the opposite for the dorsal side.

11. *Euploea algea deione* (M&F) - *Papilio slateri* (M)

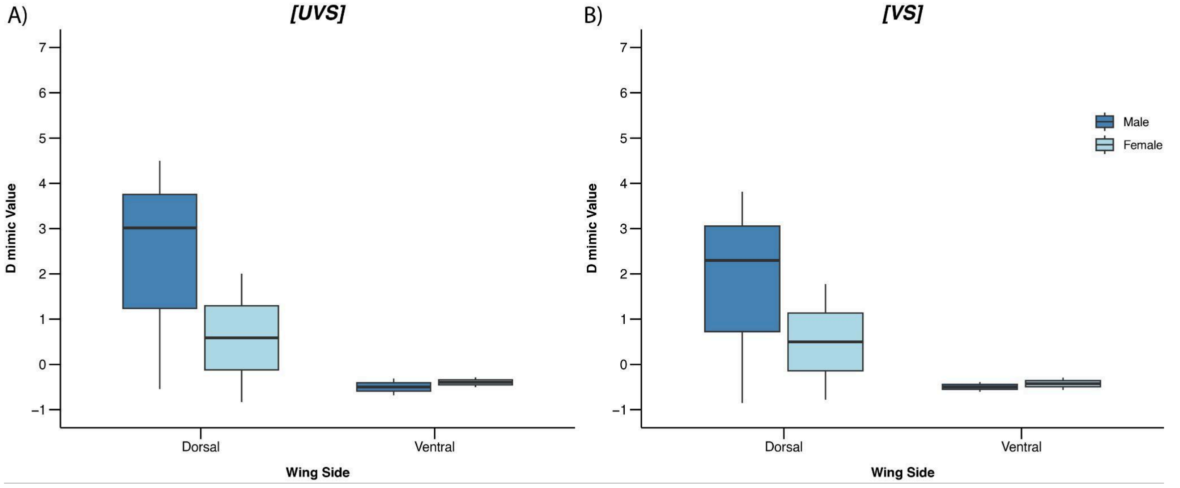


Figure 22: Relative discriminability (D_{mimic}) between the model *Euploea algea deione* (Male & Female) and the mimic *Papilio slateri* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 22), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the VS has lower D_{mimic} values compared to UVS for the dorsal side but nearly the same for the ventral side. However, the statistical tests indicated that the differences were not statistically significant. The comparison of the mimic to the female model overall had lower values as compared to the male models.

12. *Euploea midamus rogenhoferi* (M&F) - *Papilio slateri* (M)

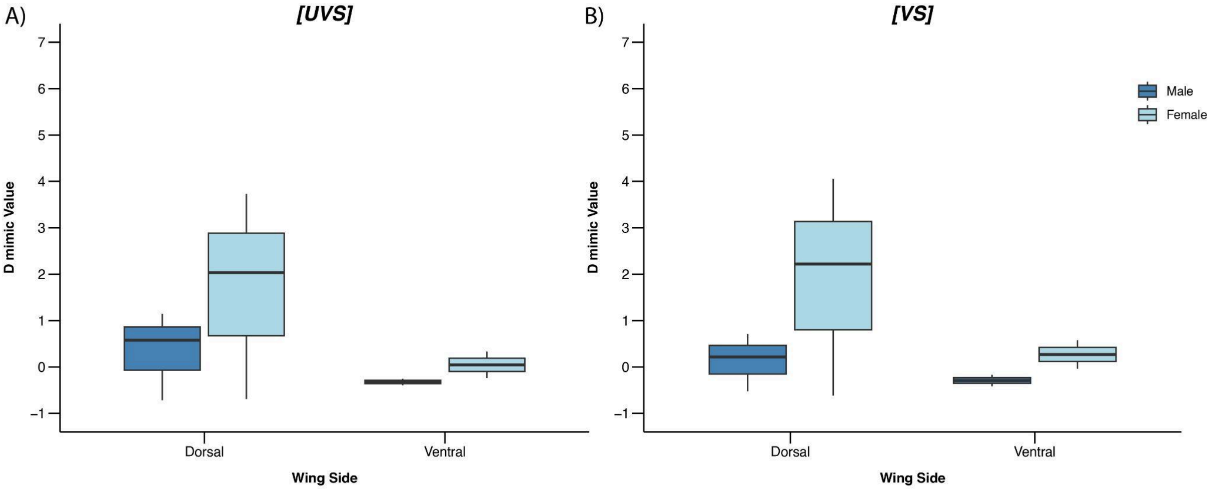


Figure 23: Relative discriminability (D_{mimic}) between the model *Euploea midamus rogenhoferi* (Male & Female) and the mimic *Papilio slateri* (Male) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 23), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the VS has lower D_{mimic} values compared to UVS for the comparison of the mimic to the male model, but opposite for the comparison to the female model. However, the statistical tests indicated that the differences were not statistically significant. The comparison of the mimic to the male model had lower values as compared to the female models for the dorsal but the opposite for the ventral side.

13. *Euploea mulciber mulciber* (M) - *Papilio slateri* (M)

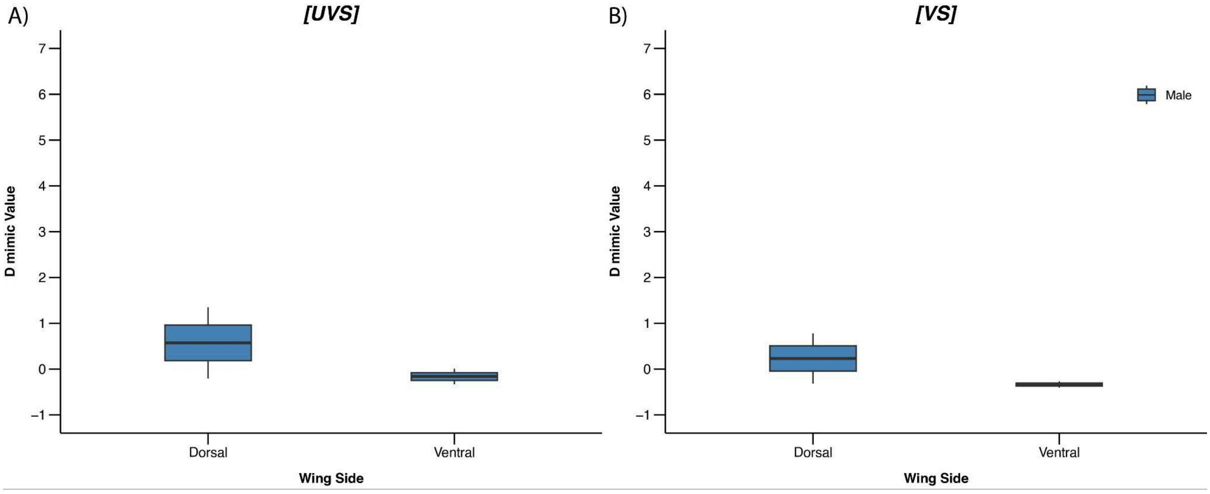


Figure 24: Relative discriminability (D_{mimic}) between the model *Euploea mulciber mulciber* (Male) and the mimic *Papilio slateri* (Male) using avian (A) UVS and (B) VS visual

Under both vision models (Figure 24), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the VS has lower D_{mimic} values compared to UVS for the dorsal side and the opposite for the ventral side. However, the statistical tests indicated that the differences were not statistically significant.

14. *Euploea klugii klugii* (M) - *Papilio slateri* (M)

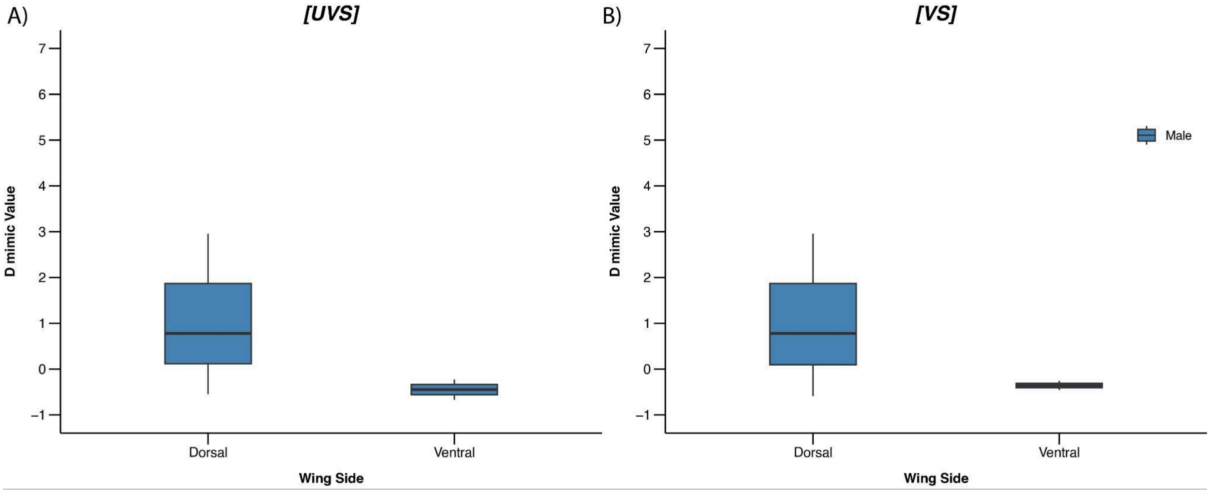


Figure 25: Relative discriminability (D_{mimic}) between the model *Euploea klugii klugii* (Male) and the mimic *Papilio slateri* (Male) using avian (A) UVS and (B) VS visual

Under both vision models (Figure 25), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the VS has lower D_{mimic} values compared to UVS. However, the statistical tests indicated that the differences were not statistically significant.

15. *Euploea sylvester hopei* (M&F) - *Papilio slateri* (M)

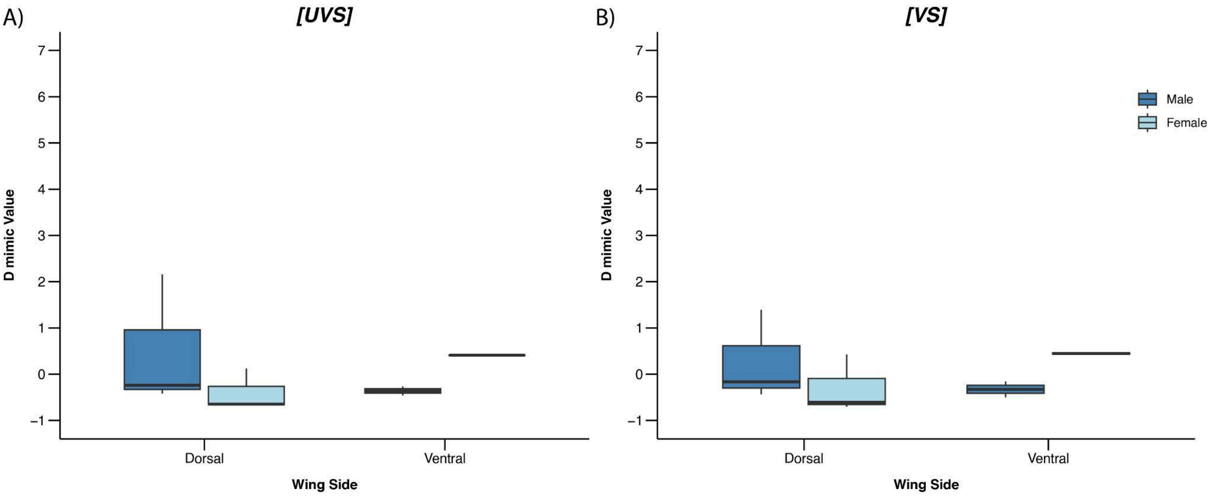


Figure 26: Relative discriminability (D_{mimic}) between the model *Euploea sylvester hopei* (Male & Female) and the mimic *Papilio slateri* (Male) using avian (A) UVS and (B) VS visual system.

Under both vision models (Figure 26), the ventral side had lower D_{mimic} values than the dorsal side. However, the statistical tests indicated that the differences were not statistically significant. The two vision models had nearly the same D_{mimic} values. The comparison of the mimic to the female model overall had lower values as compared to the male models.

Summary: Euploea Blue Mimicry Ring

The model mimic pairs in this ring had a generally lower Dmimic value for the ventral wing surface than the dorsal side under the UVS and VS visual model system. Although there were slight differences between vision models, such as lower D_{mimic} value under UVS for some pairs and under VS for some pairs, but nearly the same overall, none of these differences were statistically significant.

Comparisons involving both male and female models revealed that the mimic tended to resemble both the model equally with few exceptions. However, the dorsal and the ventral surfaces were significantly different for the comparison of male mimic *Elymnias malelas malelas* to the male model of *Euploea midamus rogenhoferi* and *Euploea sylvester hopei,* also the male mimic *Papilio slateri* to the male model *Euploea midamus rogenhoferi*.

3.3 Euploea Blue Female Mimicry Ring

The D_{mimic} values of each model mimic pair, the values after the Wilcoxon signed-rank test for the comparison under different visual models and the Wilcoxon rank-sum test for comparing the two surfaces have been tabulated.

The D_{mimic} values of the dorsal and the ventral side of each pair were compared under the two avian vision models (UVS and VS) and plotted.

			UVS	**VS**
Model	**Mimic**	**Wing Side**	**Female Dmimic (Mean± SD)**	**Female Dmimic (Mean± SD)**
Euploea mulciber mulciber (F)	*Elymnias malelas malelas* (F)	Dorsal	1.70±1.34	2.20±2.05
		Ventral	0.66±0.66	1.03±1.22

Table 8: Relative discriminability (D_{mimic}) values for Euploea blue female mimicry ring. The last two columns mention the model sex compared to the mimic.

Model	**Wing Side**	**Mimic**	
		Elymnias malelas malelas (F)	
		p-value	**V**
Euploea mulciber mulciber (F)	Dorsal	0.625	3
	Ventral	0.5	1

Table 9: Wilcoxon signed-rank test values for comparison of wing side perception under UVS and VS vision model in the Euploea blue female mimicry ring

Model	**Wing Side**	**Mimic**	
		Elymnias malelas malelas	
		p-value	**W**
Euploea mulciber mulciber (F)	UVS	0.4	9
	VS	0.4	9

Table 10: Wilcoxon rank-sum test values for comparison of dorsal and ventral sides under a fixed vision model in the Euploea blue female mimicry ring

1. *Euploea mulciber mulciber* (F) - *Elymnias malelas malelas* (F)

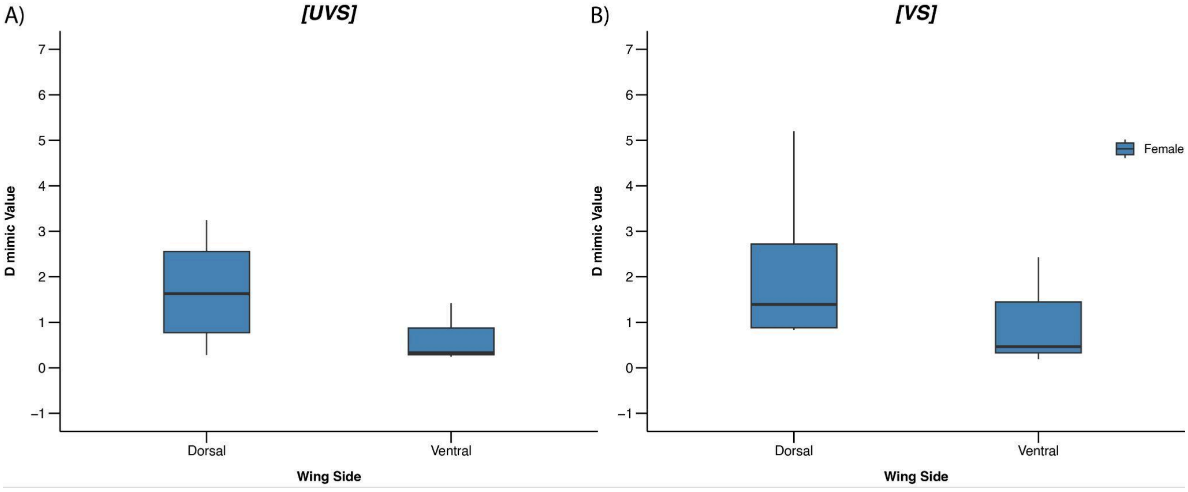


Figure 27: Relative discriminability (D_{mimic}) between the model *Euploea mulciber mulciber* (Female) and the mimic *Elymnias malelas malelas* (Female) using avian (A) UVS and (B) VS visual system

Under both vision models (Figure 27), the ventral side had lower D_{mimic} values than the dorsal side. Between the two vision models, the UVS has lower D_{mimic} values compared to VS. However, the statistical tests indicated that the differences were not statistically significant.

Summary: Euploea Blue Female Mimicry Ring

The model mimic pairs in this ring had a lower D_{mimic} value for the ventral wing surface than the dorsal side under UVS and VS visual model systems. D_{mimic} value was lower under the UVS vision model than under VS, but this difference was not statistically significant.

Chapter 4: Discussion

In this study, we aimed to see how well the Batesian mimic mimicked the aposematic colour of the model. Relative discriminability (D_{mimic}) was computed for each pair to determine how distinguishable the mimics are from the model compared to the natural variation among the model species.

4.1 Relative discriminability (D_{mimic})

A mimic colour should ideally fall within the natural variation among the model individuals, making it harder for the predators to distinguish between the two. The lower the value of the D_{mimic}, the stronger the mimicry would be, as it would indicate that the mimic is more similar to the model than the model individuals are to each other. D_{mimic} is calculated in the units of JNDs, and a JND lower than three is considered a good measure to conclude that the colour is not distinguishable from each other (Olsson et al., 2015; Siddiqi et al., 2004).
A negative D_{mimic} value might indicate that the mimic is better than the models compared to each other.

In the Danaus mimicry ring, referring to Table 2, the D_{mimic} values of each comparison were below three, except the dorsal side of both the mimic *Elymnias hypermnestra undularis* female and *Argynnis hyperbius hyperbius* female compared to the model *Cethosia biblis tisamena* male, under both vision (UVS: 4.12±5.49,4.53±5.84 and VS: 3.75±5.26,4.08±5.66). Notably, the D_{mimic} values of the comparison between the model *Danaus chrysippus* male with both the mimics *Elymnias hypermnestra undularis* female and *Argynnis hyperbius hyperbius* female were less than 1, indicating the very strong similarity of colour.

In Euploea blue ring, referring to Table 5, the D_{mimic} value of the model mimic comparison for each pair is well below three, except the dorsal side of mimic *Elymnias patna* male with the female model *Euploea midamus rogenhoferi* and male model *Euploea klugii klugii*, under both UVS and VS vision systems (UVS:

4.27±2.67, 3.66±1.25 and VS: 4.71±2.74, 3.57±1.66). Overall, *Papilio slateri* has the lowest D_{mimic} values, suggesting that it is the most effective mimic in the mimicry ring. In the Euploea blue female ring, referring to Table 8, the D_{mimic} values are also low, indicating a strong mimetic resemblance in all comparisons.

In all the rings, the mimics show good mimetic resemblance to the models, and therefore, the colour of their wings is not distinguishable from that of the avian predators under both UV and VS vision systems.

4.2 Extent of resemblance on the Dorsal and Ventral side of the wing

In section 4.1, we observed that the D_{mimic} values of all comparisons except a few are lower than three, making them not discriminable. And when the two surfaces were compared, the ventral D_{mimic} values were generally lower than the dorsal, indicating better mimicry on the former side.

In butterflies, different wing surfaces serve different ecological functions, influencing how mimicry evolves. From a mimic's perspective, investing in resembling the most visible surface of the aposematic model to the predator might offer a better adaptive benefit. The dorsal surface, which is exposed during flight to the hunting avian predator, making it more vulnerable, could be under selective pressure to resemble the model closely to avoid detection by avian predators in motion. However, butterflies also spend a substantial amount of time resting with their wings closed during the day when the avian predators are active. In such cases, the ventral surface would be more visible to them, subjecting it to a stronger selective pressure for accurate mimicry.

It has been observed that the ventral surfaces are often associated with predator avoidance while the dorsal surface is used for sexual signalling (Oliver et al., 2009). In the mimicry rings of Western Ghats, the mimics showed a greater extent of resemblance of the ventral surface (Su et al., 2015). These might support the idea that the mimicry on the ventral side may be more strongly selected than the dorsal side.

However, the statistical test indicates an absence of a significant difference between the two surfaces for each model mimic pair. The dorsal and the ventral side of the mimic *Elymnias patna* with the model *Euploea midamus rogenhoferi* and *Euploea klugii klugii* had significant differences (Wilcoxon rank-sum test, $p<0.05$). This indicates that among all the models, the ventral side of these are more significantly different from the dorsal side. One of the reasons why the ventral surface of *Elymnias patna* might be more discriminable is that it is cryptic on the ventral side and hence does not closely resemble the models of the mimicry ring.

The absence of significance in the difference might indicate that the dorsal and the ventral sides show comparable levels of precision in mimicry, with neither side outperforming the other. This could suggest that the mimics have come to imitate the models equally well from both sides to avoid the predators over the years. Although the mimicry relies heavily on the aposematic colour, the pattern, wing shape, and flight morphology of the species are also some factors that would affect this phenomenon. Lastly, the lack of significance might also be influenced by the limited sample size due to logistical constraints.

4.3 Extent of resemblance between avian UVS and UV vision system

In *Heliconius* butterflies, it was observed that UVS birds could detect differences between the comimics and the conspecifics better than the VS birds, suggesting that mimicry is more effective against VS predators (Dell'Aglio et al., 2018). Few butterflies also have UV-sensitive colour patches on the body, which the VS predators might be unable to detect. However, in this study, all three mimicry rings had no statistical difference between the D_{mimic} values between the UVS and the VS vision system for all model mimic pairs. This might suggest that the colour differences perceived under both visual models are similar, implying that the mimics' colours are perceived equally well or equally poorly by the birds with either type of visual system. Hence, the mimicry success may not strongly depend on whether the predator has UVS or VS vision. Another reason might be that the species in the mimicry rings of this study did not have any unique UV patch, making them identical in the eye of the avian predators with both kinds of vision.

It might also be that the mimic has evolved a broad spectrum resemblance that works for both the avian visual systems over niche-specific optimization. Since the North-East is a biodiversity hotspot, it houses many bird species with different visual systems. Hence, having such a broad-spectrum resemblance would give the prey a survival advantage.

4.4 Extent of resemblance of the mimic to the male and the female model

We often see many mimicry rings like that in the Danaus mimicry ring (Figure 1), which has female-limited mimics. Females face greater predation risk because they bear an egg load, impairing their flight speed (Marden & Chai, 1991; Ohsaki, 1995). This drives the selection for stronger aposematic signals for survival advantage. However, in a monomorphic model system where both sexes serve as a model, we tried to observe if a certain sex is preferred more than the other by the mimic. In this study, we noticed that in most monomorphic model system comparisons, the mimics closely resembled the female model more than its male counterpart in the Danaus mimicry ring. However in the Euploea blue mimicry ring the comparisons were not that different hence are seen to mimic either model equally.

One explanation for this pattern could be that female models provide a more consistent and reliable signal for the predators to learn from as they spend a large amount of time during oviposition. This, in turn, makes them a reliable source for the mimics to learn from. Additionally, the males of the model species might also be subjected to stronger sexual selection, which might make their wing colouration variable and hence less associated with the aposematic signal, favouring the mimicry of female signalling.

An alternative possibility could be where males serve as better models due to their greater abundance in nature. This higher encounter rate might provide a good training model for the mimics to learn aposematic signals from, making them a better model. However, in this study, the closer resemblance to female models might suggest that signal consistency and exposure time may play a stronger role in shaping mimetic resemblance.

4.5 Summary

This study observed that all the mimics closely resemble the model's aposematic colours, making them indistinguishable to the UVS and VS avian predators. All the wing surfaces had values generally lower than three, but comparing the two surfaces, the ventral seemed to have lower values. Suggesting that the ventral surface might have a greater role in predator avoidance. UVS and VS avian predators appeared to perceive the colour equally for each side. In a monomorphic model system, the mimics more closely resembled the female model. These findings reflect on how mimicry might work in the mimetic communities of North-East India and how certain aspects might affect the evolution of mimicry.

4.6 Future directions

Due to its time constraints and the seasonal nature of butterflies, this study couldn't sample all the species within a mimicry ring. Future work should include a larger study sample to strengthen the conclusions drawn. Other aspects, like flight morphology and wing pattern, also offer deeper insight into the forces driving the mimetic resemblance, which should be studied. Various moths in the mimicry ring could also be considered, as they are known to be more toxic than butterflies and might serve as a primary model. Finally, the North-East has many mimicry rings that could not be added due to logistical reasons. Hence, future studies can also include these to provide a broader understanding of how mimicry evolves across the evolutionary timescale.

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