Prey from the eyes of predators: Color discriminability of aposematic and mimetic butterflies from an avian visual perspective

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Predation exerts strong selection on mimetic butterfly wing color patterns, which also serve other functions such as sexual selection. Therefore, specific selection pressures may affect the sexes and signal components differentially. We tested three predictions about the evolution of mimetic resemblance by comparing wing coloration of aposematic butterflies and their Batesian mimics: (a) females gain greater mimetic advantage than males and therefore are better mimics, (b) due to intersexual genetic correlations, sexually monomorphic mimics are better mimics than female-limited mimics, and (c) mimetic resemblance is better on the dorsal wing surface that is visible to predators in flight. Using a physiological model of avian color vision, we quantified mimetic resemblance from predators' perspective, which showed that female butterflies were better mimics than males. Mimetic resemblance in female-limited mimics was comparable to that in sexually monomorphic mimics, suggesting that intersexual genetic correlations did not constrain adaptive response to selection for female-limited mimicry. Mimetic resemblance on the ventral wing surface was better than that on the dorsal wing surface, implying stronger natural and sexual selection on ventral and dorsal surfaces, respectively. These results suggest that mimetic resemblance in butterfly mimicry rings has evolved under various selective pressures acting in a sex- and wing surface-specific manner.

Evolution of animal signals is influenced by a combination of selective pressures. For instance, in dendrobatid frogs and *Heliconius* butterflies, color patterns that serve as aposematic and mimetic visual signals directed toward the predators may also serve as sexual signals (Jiggins et al. 2004; Maan and Cummings 2009; Finkbeiner et al. 2014). As a result, signals may evolve to optimize the sum of their functions, at a cost to signal efficacy in any one dimension; for example when two or more mimetic species coexist, courtship may sometimes be directed toward members of another species due to mistaken species identity, which may represent a cost of mimetic convergence (Estrada and Jiggins 2008). Similarly, sexual selection on butterfly wing patterns may drive the evolution of imperfect mimicry or sex-limited mimicry (Krebs and West 1988; Codella and Lederhouse 1989;

Lederhouse and Scriber 1996). The strength and nature of signals may also differ in a sex-specific manner since natural and sexual selection may act differentially on males and females (Kemp 2008; Maan and Cummings 2009; Rojas and Endler 2013). Furthermore, signals may evolve to convey specific information to intended receivers, such that different wing surfaces in butterflies serve different functions with respect to natural and sexual selection (Oliver et al. 2009).

In this article, we investigate how signals (i.e., wing coloration) have evolved in mimetic butterfly communities called mimicry rings, which are composed of Müllerian comodels (toxic species) and Batesian mimics. Since the evolution of mimetic signals is influenced concurrently by natural and sexual selection as discussed above, we formulated and tested the following three

predictions in these butterfly mimicry rings: (a) Females are better mimics: female butterflies apparently experience greater predation risk than males (Ohsaki 1995), hence females may gain more from mimicry. Also, males may face stronger sexual selection, which may constrain the mimetic resemblance of male wing coloration (Krebs and West 1988; Lederhouse and Scriber 1996). As a result of both the processes, females may show greater mimetic resemblance than males. (b) Sexually monomorphic mimics show greater mimetic resemblance than female-limited mimics: In some species, only females are mimetic whereas males show non-mimetic ancestral coloration (Kunte 2008). Since sex-specific selection on wing coloration may be hampered by genetic correlations between the sexes (Lande 1987), mimetic resemblance in female-limited mimics may be constrained and thus be lower than that in monomorphic mimics. (c) Dorsal wing surfaces show better mimetic resemblance than ventral surfaces: aerially hunting visual predators such as insectivorous birds are considered to be the primary selective agents of butterfly mimicry (Chai 1996; Pinheiro 2003, 2011; Langham 2004, 2006). Since dorsal wing surfaces of butterflies are exposed and visible to predators during flight, dorsal wing surfaces should show better mimetic resemblance than ventral wing surfaces.

We tested these hypotheses by quantifying butterfly mimetic resemblance from predators' perspective using objective measurements of butterfly wing coloration and a physiological model of avian color vision. This methodological departure from most previous studies is an important one as prior assessments of butterfly mimicry were largely based on human perception, which can be misleading due to differences in visual capabilities between humans and birds (Bennett et al. 1994). Only a few studies have recently used such methods to examine color signals in aposematic and mimetic butterflies from predators' perspective (Bybee et al. 2012; Stobbe and Schaefer 2008; Llaurens et al. 2014). Unlike humans, birds are sensitive to ultraviolet wavelengths (300–400 nm; Bennett and Cuthill 1994; Cuthill et al. 2000) and possess tetrachromatic color vision (Maier and Bowmaker 1993; Osorio et al. 1999). Avian cones also contain pigmented oil droplets that narrow their spectral sensitivity functions (Hart et al. 1998, 2000a, b), resulting in better color discriminability and constancy (Vorobyev et al. 1998; Vorobyev 2003; Stavenga and Wilts 2014). As a result, birds are able to perceive a greater range and diversity of colors than humans, making human assessment an inaccurate representation of avian perception (Cherry and Bennett 2001; Eaton 2005; Håstad and Ödeen 2008; but see Seddon et al. 2010). By analyzing butterfly wing coloration using avian perception, we show that mimetic resemblance in butterfly mimicry rings has indeed evolved in a sex- and wing surface-specific manner in response to various selective pressures.

Methods

BUTTERFLY MIMICRY RINGS

There are seven butterfly mimicry rings in the Western Ghats of south-western India that comprise toxic models and Batesian mimics (Kunte 2000). Both the models and the mimics in these mimicry rings belong to families Papilionidae, Pieridae, and Nymphalidae. Mimicry rings are here named after the most common model species in each mimicry ring (e.g., (*Danaus*) *genutia*), and when more than one model species is common, after the genus name of the predominant models (e.g., *Tirumala*). In total, there are 14 models, all of which appear to have sexually monomorphic wing color patterns, and 12 Batesian mimics, out of which four show sexually monomorphic mimicry while the remaining eight exhibit female-limited mimicry. Model-mimic relationships in all the mimicry rings are shown in Table 1 and Figure S1. Aposematism of the models and the model-mimic relationships in some of these mimicry rings have been tested with experiments on predators (Larsen 1992, 2007; Uesugi 1995, 1996). Model-mimic relationships involving *Danaus* (Edmunds 1966; Smith 1973, 1976; Smith and Gordon 1987; Gordon et al. 2010) and *Pachliopta* models (Uesugi 1995, 1996; Kitamura and Imafuku 2010) have been particularly well studied. In the remaining mimicry rings, we presume the model-mimic relationships as defined previously to be reliable based on the natural history information on larval host plants, plant chemistry, and behavior and phenotypes of butterfly caterpillars and adults (Wynter-Blyth 1957; Kunte 2000). A thorough experimental investigation of model-mimic relationships of the Western Ghats butterflies will be useful but this is beyond the scope of this work.

SPECTRAL MEASUREMENTS

We measured reflectance spectra of butterfly specimens deposited in the Collections Facility at NCBS and at the Natural History Museum, London. Details of butterfly specimens and sample sizes are given in Table 1. In total, we took more than 3000 spectral readings from over 200 specimens. All the specimens used were pinned, with wings spread out. We measured wing reflectance using an Ocean Optics Jaz spectrometer with illumination provided by a PX-1 pulsed xenon lamp (Dunedin, FL, USA). We used two optical fibers (both outfitted with a collimating lens): the illuminating fiber was positioned at 90° to the horizontal wing surface to produce a small illumination spot (approximately 1 mm in diameter) and the collecting fiber was set at 45° to minimize glare. Since the wing colors measured were pigmentary and not structural, the angle of the collecting fiber (i.e., 45°) was unlikely to influence reflectance measurements significantly. The illuminating and collecting probes were aligned in the same vertical plane that was perpendicular to both the horizontal wing surface

Table 1. Number of specimens measured of each butterfly species in this study (N.A. = not applicable in case of males of female-limited mimetic species. * = female-limited mimetic species).

Mimicry ring	Butterfly species	Model/mimic	No. of males measured	No. of females measured
chrysippus	*Danaus c. chrysippus*	Model	5	5
	*Hypolimnas misippus**	Mimic	N.A.	4
genutia	*Danaus g. genutia*	Model	3	4
	Cethosia mahratta	Model	2	3
	*Elymnias caudata**	Mimic	N.A.	4
	*Argynnis castetsi hybrida**	Mimic	N.A.	1
eucharis	*Delias eucharis*	Model	5	5
	Prioneris sita	Mimic	2	1
Pachliopta	*Pachliopta pandiyana*	Model	1	5
	Pachliopta a. aristolochiae	Model	10	10
	*Papilio polytes romulus, f. stichius**	Mimic	N.A.	20
hector	*Pachliopta hector*	Model	10	10
	*Papilio polytes romulus, f. romulus**	Mimic	N.A.	20
Euploea	*Euploea c. core*	Model	5	5
	Euploea klugii kollari	Model	1	5
	Euploea sylvester coreta	Model	5	5
	*Hypolimnas bolina jacintha**	Mimic	N.A.	5
	Papilio clytia, f. clytia	Mimic	1	4
	Papilio dravidarum	Mimic	2	2
Tirumala	*Tirumala limniace exoticus*	Model	5	1
	Tirumala septentrionis dravidarum	Model	5	5
	Parantica a. aglea	Model	3	2
	Parantica nilgiriensis	Model	5	1
	Papilio clytia, f. dissimilis	Mimic	2	4
	*Pareronia ceylanica ceylanica**	Mimic	N.A.	1
	*Pareronia hippia**	Mimic	N.A.	5

and the long axis of the butterfly's body. We placed individual butterfly specimens on a vertical translation stage and adjusted the distance between the wing surface and the illuminating probe until the maximum reflectance was obtained. We measured spectra relative to a Spectralon reflectance standard (Ocean Optics), which reflects >96% of incident light.

We categorized markings with the same color on forewings and/or hindwings as a single color patch because they were found to have highly similar reflectance, and took two to eight spectral measurements per color patch depending on its extent on the wing. For each mimicry ring, we measured spectral readings of different butterfly species from corresponding wing regions. For each color patch, we used averaged reflectance values between 300 and 700 nm of each individual (see Visual Modeling). Considering the color patterns of various mimicry rings, we measured two colors on the dorsal side and two colors on the ventral side in each mimicry ring. The two exceptions were: (a) the *genutia* mimicry ring, which had two color patches only on the dorsal side because mimics in this ring are not mimetic on the ventral side (Fig. S1), and (b) the *eucharis* mimicry ring, which had one dorsal and three

ventral color patches. We did not include black wing patches in the analyses because they generally showed very low reflectance (i.e., <5%), but the reflectance of all other wing colors were measured and analyzed. The color patches for each mimicry ring and the reflectance spectra of each butterfly species are shown in Figure S2.

VISUAL MODELING OF AVIAN COLOR VISION
Avian color vision is mediated by four classes of single-cone photoreceptors: long-wavelength sensitive (LWS), medium-wavelength sensitive (MWS), short-wavelength sensitive (SWS), and ultraviolet/violet sensitive (UVS/VS) (Hart and Hunt 2007). The peak sensitivities of LWS, MWS, and SWS photoreceptors are highly conserved across avian taxa. On the other hand, the spectral sensitivity of UVS/VS photoreceptors peaks either near 370 nm (UVS) or 410 nm (VS) (Hart 2001), thus avian vision is categorized either as UVS or VS. Insectivorous birds in the Western Ghats include drongos (Dicruridae), bee-eaters (Meropidae), and flycatchers (Muscicapidae) (Ali and Ripley 2002). Dicruridae

and Meropidae have VS vision, whereas Muscicapidae have UVS vision (Ödeen et al. 2011; Ödeen and Håstad 2013).

RECEPTOR NOISE MODEL

We used the receptor noise model (Vorobyev and Osorio 1998; Vorobyev et al. 1998, 2001) to estimate color discriminability from an avian visual perspective. According to this model, the quantum catch Q_i for each cone type i is first calculated as a function of the photoreceptor spectral sensitivity (S_i), the irradiance spectrum incident on the color patch (I), and the reflectance spectrum of the patch (R) over the visible spectrum (i.e., 300–700 nm):

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

According to Fechner's law, the receptor signal f_i of cone type i is proportional to the logarithm of the quantum catch; the difference in receptor signal Δf_i between two colors A and B is hence given by:

$$\Delta f_i = f_{iA} - f_{iB} = \ln Q_{iA} - \ln Q_{iB} = \ln \frac{Q_{iA}}{Q_{iB}} \, .$$

Receptor noise for each cone type i is defined by the noise-to-signal ratio known as the Weber fraction (ω_i), which is derived from the noise-to-signal ratio of a single receptor (v_i) and the relative number of each receptor type (n_i):

$$\omega_i = \frac{v_i}{\sqrt{n_i}} \, .$$

Color discrimination using all four cone types in an avian tetrachromatic visual system is then calculated using the following equation:

$$\Delta S = \sqrt{ \frac{ \left[\begin{matrix} (\omega_1\omega_2)^2(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2(\Delta f_4 - \Delta f_2)^2 + (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2)^2 + \\ (\omega_2\omega_3)^2(\Delta f_4 - \Delta f_1)^2 + (\omega_2\omega_4)^2(\Delta f_3 - \Delta f_1)^2 + (\omega_3\omega_4)^2(\Delta f_2 - \Delta f_1)^2 \end{matrix} \right] }{ (\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2 } } \, .$$

The color distance ΔS, given in units of "just noticeable difference" (jnd), describes the perceptual distance between two spectra, such that the higher the value, the more distinguishable the two colors are from an avian visual perspective.

We modeled avian perception using the averaged spectral sensitivities of both UVS and VS visual systems (Endler and Mielke 2005). Standard daylight ("D65") was used as the irradiance spectrum, and receptor noise was determined using the retinal cone proportions of the well-studied blue tit *Cyanistes caeruleus* (1:1.92:2.68:2.7 for SWS1:SWS2:MWS:LWS cones; Hart et al. 2000a). Lastly, we used a Weber fraction of 0.05 for the most abundant receptor type, following recently published studies (Langmore et al. 2011; Stoddard and Stevens 2011; Antonov et al. 2012; Delhey et al. 2013). All modeling was performed using the R package Pavo (Maia et al. 2013).

RELATIVE DISCRIMINABILITY

In the Western Ghats mimicry rings, toxic models appear largely sexually monomorphic to humans. However, due to differences in visual capabilities, birds may be able to perceive differences in wing coloration of male and female models. To determine whether avian predators can discriminate between the sexes, we used the approach given in Håstad et al. (2005) to derive the relative discriminability of male and female models. For each model species, we first calculated the average intrasexual color distance (ΔS_a) and the average intersexual color distance (ΔS_b). Relative discriminability of male and female models was then derived as follows:

$$D_{\mathrm{model}} = \frac{\Delta S_b - \Delta S_a}{\sqrt{\Delta S_a}} \, .$$

Higher D_{model} values signify that male and female models are discriminable to birds.

Next, to determine whether avian predators can discriminate between mimics and models, we calculated the average interspecific color distance between the mimic and its model (ΔS_c) and the average intraspecific color distance within model conspecifics (ΔS_d). Relative discriminability of the mimic against the model was then given by:

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

Thus, relative discriminability of mimic against model (i.e., converse of D_{mimic}) provided a measure of mimetic resemblance, with lower D_{mimic} values indicating better mimetic resemblance.

STATISTICAL ANALYSES

D_{mimic} values for each mimic-model pair are given in Tables S2–S6, and Figure S3. Males and females of some model species were discriminable from an avian visual perspective (i.e., dimorphic models with $D_{\mathrm{model}} > 0$ for some or all color patches), while males and females of other model species could not be discriminated (i.e., monomorphic models with $D_{\mathrm{model}} \leq 0$ for all color patches) (Table S1). Therefore, we calculated relative

discriminability D_{mimic} for mimics with respect to male and female models separately. Also, for sexually monomorphic mimics, we calculated D_{mimic} for male and female mimics separately (D_{mimic} was calculated only for females in case of female-limited mimicry). We made approximately 16,300 pairwise comparisons of spectral differences between color patches, sexes, and species to calculate color distance and relative discriminability between mimics and models. The distributions of relative discriminability values were positively skewed, with values of $0 < D_{mimic} < 1$ being the most common. As D_{mimic} values were not normally distributed (Shapiro–Wilk test), we used Wilcoxon rank-sum tests and Wilcoxon signed-rank tests for all pairwise comparisons. Statistical analyses were performed in R (R Core Team 2013).

Results

D_{mimic} values for females of sexually monomorphic Batesian mimics were significantly lower than those for males (UVS: dorsal: ♂ = 3.62 ± 3.02; ♀ = 2.60 ± 2.67; ventral: ♂ = 2.34 ± 2.78; ♀ = 1.84 ± 2.17; VS: dorsal: ♂ = 3.69 ± 3.02; ♀ = 2.36 ± 2.59; ventral: ♂ = 2.51 ± 3.01; ♀ = 1.71 ± 2.34), indicating that females had better mimetic resemblance as compared to males (UVS: Wilcoxon signed-rank test: dorsal: $V = 55$, $P < 0.001$; ventral: $V = 190$, $P < 0.01$; Fig. 1A; VS: Wilcoxon signed-rank test: dorsal: $V = 14$, $P < 0.001$; ventral: $V = 119$, $P < 0.001$; Fig. 1B).

Females of female-limited mimetic species had similar D_{mimic} values as females of sexually monomorphic mimics (UVS: dorsal: ♀-limited mimics = 3.10 ± 3.36; monomorphic ♀ = 2.60 ± 2.67; ventral: ♀-limited mimics = 2.44 ± 3.40; monomorphic ♀ = 1.84 ± 2.17; VS: dorsal: ♀-limited mimics = 2.14 ± 2.85; monomorphic ♀ = 2.36 ± 2.59; ventral: ♀-limited mimics = 2.60 ± 3.90; monomorphic ♀ = 1.71 ± 2.34), suggesting that mimetic resemblance in female-limited mimics was as good as that in females of monomorphic mimics (UVS: Wilcoxon rank-sum test: dorsal: $W = 1194$, $P = 0.43$; ventral: $W = 954$, $P = 0.72$; Fig. 1A; VS: Wilcoxon rank-sum test: dorsal: $W = 1041$, $P = 0.73$; ventral: $W = 1052$, $P = 0.23$; Fig. 1B). Females of female-limited mimetic species also had similar D_{mimic} values as males of sexually monomorphic mimics in most comparisons (UVS: dorsal: ♀-limited mimics = 3.10 ± 3.36; monomorphic ♂ = 3.62 ± 3.02; ventral: ♀-limited mimics = 2.44 ± 3.40; monomorphic ♂ = 2.34 ± 2.78; VS: dorsal: ♀-limited mimics = 2.14 ± 2.85; monomorphic ♂ = 3.69 ± 3.02; ventral: ♀-limited mimics = 2.60 ± 3.90; monomorphic ♂ = 2.51 ± 3.01), implying that mimetic resemblance in female-limited mimics was comparable to that in males of monomorphic mimics (UVS: Wilcoxon rank-sum test: dorsal: $W = 934$, $P = 0.25$; ventral: $W = 860$, $P = 0.66$; Fig. 1A; VS: Wilcoxon rank-sum test: dorsal: $W = 665$, $P < 0.01$; ventral: $W = 879$, $P = 0.78$; Fig. 1B). Thus, the only avian visual system in which females of female-limited mimetic

species showed better mimetic resemblance to the models than males of sexually monomorphic mimetic species was the dorsal coloration from an avian VS perspective. Therefore, on the whole, females of female-limited mimetic species and both the sexes of monomorphic mimetic species showed largely comparable mimetic resemblance to models.

Ventral wing surfaces of butterfly mimics had significantly lower D_{mimic} values than dorsal wing surfaces (UVS: dorsal = 3.10 ± 3.11; ventral = 2.23 ± 2.87; VS: dorsal = 2.60 ± 2.89; ventral = 2.30 ± 3.22), suggesting that mimetic resemblance was better on ventral surfaces as compared to dorsal surfaces (Wilcoxon rank-sum test: UVS: $W = 9888$, $P < 0.01$; VS: $W = 9391$, $P < 0.05$; Fig. 2).

Discussion

Studies of visual mimicry have contributed substantially to understanding various evolutionary ideas, such as predation as a selective agent, adaptation, signal evolution, and frequency-dependent selection. Most studies of aposematism and mimicry traditionally assessed associated signals using human vision. However, these visual signals should be quantified objectively (i.e., by using spectrophotometers) and studied from the perspective of intended receivers (e.g., predators) to have ecological relevance (Bennett et al. 1994). This has been done recently in studies involving aposematic dendrobatid frogs and *Heliconius* butterflies (Maan and Cummings 2009; Bybee et al. 2012; Crothers and Cummings 2013; Llaurens et al. 2014), as well as avian egg mimicry (Spottiswoode and Stevens 2010; Stoddard and Stevens 2011; Antonov et al. 2012). However, studies of Batesian and Müllerian mimicry that broadly use this approach are scarce. Since insectivorous birds are the main predators of butterflies, aposematic and mimetic signals must be assessed based on the visual systems of these birds. In this article, we analyzed mimetic resemblance in butterfly mimicry rings of the Western Ghats using a physiological model of avian color vision. Intraspecific comparisons of mimetic resemblance revealed that female butterflies were better mimics than males, whereas interspecific comparisons showed that female-limited mimics were as good as sexually monomorphic mimics. Ventral wing surfaces showed greater mimetic resemblance than dorsal surfaces. These results are interesting because they point out how natural selection for mimicry may act in a sex- and wing surface-specific manner that produces diverse wing patterns.

Avian visual modeling showed that females of sexually monomorphic mimetic species were better Batesian mimics as compared to males. This may be a general pattern across different mimicry types: among *Heliconius* and *Melinaea* butterflies, females are better Müllerian mimics than males (Llaurens et al. 2014). This could be because natural and sexual selection act differentially on the sexes, which may affect the degree of mimetic
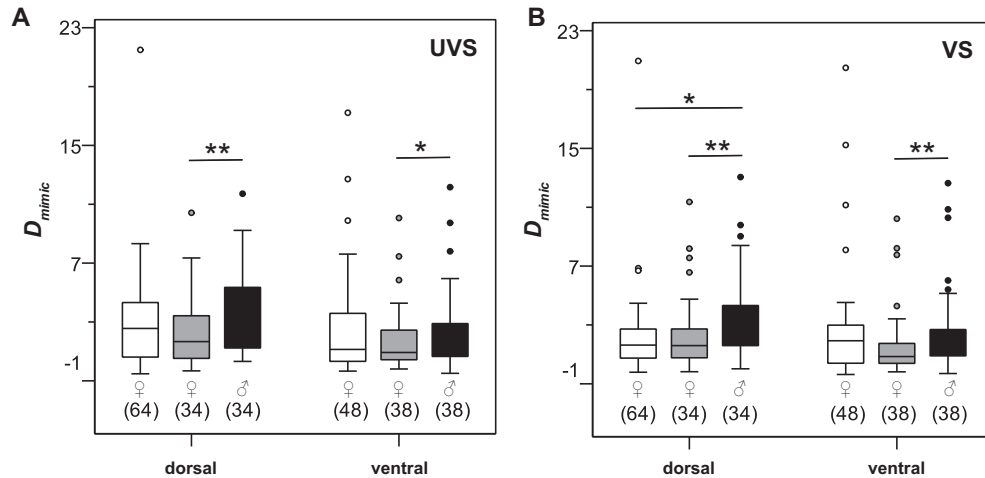
Figure 1. Pairwise comparisons of mimetic resemblance (D_{mimic}) between female-limited Batesian mimics (white) and sexually monomorphic Batesian mimics (light gray: females; dark gray: males) to their Müllerian models using avian UVS (A) and VS (B) visual systems. Numbers in parentheses indicate sample sizes. Dorsal and ventral wing surfaces are compared separately. * = $P < 0.01$; ** = $P < 0.001$.

resemblance in a sex-specific manner. There is evidence from several studies that female butterflies face greater predation risk (Kingsolver 1995a, b; Ohsaki 1995, 2005; Ide 2006) because they have a less effective escape flight due to their heavy egg-loads (Wallace 1865; Srygley and Chai 1990). Female-biased predation has also been observed in crickets (Gwynne and Dodson 1983; O'Neill and O'Neill 2003; Ercit 2014), possibly because egg-loads impair the jumping ability of females (Ercit et al. 2014). Thus, greater predation risk could select for better mimetic resemblance in females of sexually monomorphic mimics. On the other hand, male wing coloration may be under stronger sexual selection, which may act antagonistically to natural selection. Females of many butterfly species show mating preference for males with brighter and/or more saturated colors (Robertson and Monteiro 2005; Davis et al. 2007; Kemp 2007, 2008; Papke et al. 2007; Morehouse and Rutowski 2010; Rutowski and Rajyaguru 2012). In the mimetic butterfly *Papilio polyxenes*, males are less effective mimics of the toxic *Battus philenor* (Codella and Lederhouse 1989), and males with wing coloration altered to resemble a female-like mimetic pattern are less successful in establishing mating territories as compared to unaltered males (Lederhouse and Scriber 1996). Therefore, both female mate choice and male–male competition may cause mimicry to be less effective in males. Thus, better mimetic resemblance in females may be due to the combination of stronger natural selection on females and stronger sexual selection on males.

Sexual dimorphism is the evolutionary outcome of selective pressures that differ between the sexes (Cox and Calsbeek 2009). Despite the presence of sexual dimorphism, sexually dimorphic traits might still deviate from their sex-specific fitness optima due to positive intersexual genetic correlations that constrain the independent phenotypic evolution of males
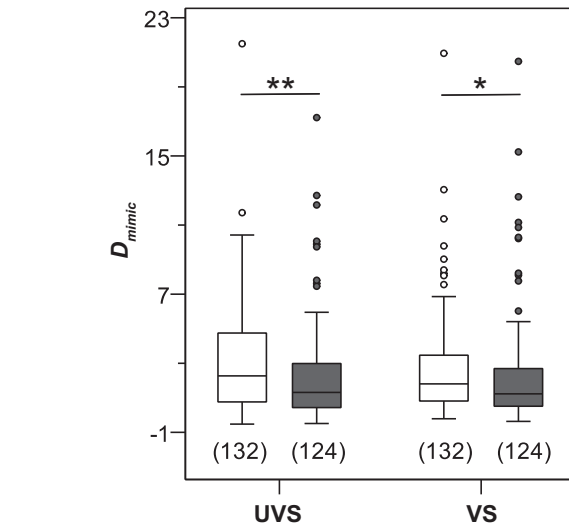
Figure 2. Mimetic resemblance (D_{mimic}) of dorsal (white) and ventral (gray) wing coloration of all mimics compared to all of their models from an avian UVS and VS visual perspective. Numbers in parentheses indicate sample sizes. * = $P < 0.05$; ** = $P < 0.01$.

and females (Price and Burley 1994; Merila et al. 1998; Poissant et al. 2009). In light of this, we expected female-limited mimics to show a lesser degree of mimetic resemblance as compared to sexually monomorphic mimics. However, our findings suggested that natural selection for female-limited mimicry was sufficiently strong to overcome intersexual genetic correlations between mimetic females and nonmimetic males, to the extent that the degree of mimetic resemblance shown by female-limited mimics was as good as that shown by sexually monomorphic mimics.

In addition to being sex-specific, selection could also act in a wing surface-specific manner. Dorsal wing surfaces of aposematic and mimetic butterflies are exposed during flight and are easily spotted by their primarily aerially hunting bird predators, so we expected dorsal coloration to exhibit greater mimetic resemblance. Contrary to our prediction, ventral wing surfaces of Batesian mimics showed a better match to the aposematic signal of their models in the Western Ghats butterfly mimicry rings. This could evolve from differential natural and sexual selection on the two wing surfaces. In many butterflies, dorsal wing patterns are typically used for sexual signaling while ventral coloration is used for predator avoidance (Codella and Lederhouse 1989; Lederhouse and Scriber 1996; Breuker and Brakefield 2002; Balint et al. 2009; Oliver et al. 2009; Rutowski et al. 2010). It is possible that even aposematic and mimetic butterflies face considerable predation risk at rest rather than in flight, similar to *Bicyclus* and other butterflies that rest on the forest floor and low vegetation during most of the day when avian predators are active. Additionally, motion blur during flight may relax selection for perfect mimicry on the dorsal wing surface, whereas better mimicry on the ventral wing surface may confer a considerable selective advantage to butterflies at rest. Therefore, stronger sexual selection operating on the dorsal wing surface and stronger natural selection for Batesian mimicry on the ventral surface may explain the wing surface-specific difference in mimetic resemblance found in this study.

Majority of previous studies on mimicry rings focused predominantly on the Müllerian component and largely ignored the Batesian component. However, mimicry ring-wide evolution of aposematic signals and mimetic resemblance must be a result of dynamics that involve both Müllerian and Batesian components. Our study is one of the first to consider both the components of mimicry rings, in which we quantified butterfly mimetic resemblance using objective color measurements and avian visual modeling. We showed that mimetic resemblance between Batesian mimics and their toxic models may be influenced by sex- and wing surface-specific selection pressures. Future studies that account for other factors may provide additional insights into how the sexes and wing surfaces respond to selection for mimicry in a specific manner. Apart from coloration, wing patterns, i.e., spatial arrangement of markings (Stoddard 2012; Taylor et al. 2013), locomotor mimicry (Srygley and Ellington 1999; Srygley 2004; Kitamura and Imafuku 2010), and color generalization by predators (Exnerová et al. 2006; Ham et al. 2006; Svádová et al. 2009; Sandre et al. 2010; Kazemi et al. 2014) may influence mimetic resemblance and subsequent protection from predators. It may be fruitful to apply our findings in designing behavioral experiments that test the ideas presented above using real predators, their sensory perception, and their fitness consequences for mimics.

DATA ARCHIVAL
Presented as supplementary online material associated with this manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Intersexual relative discriminability of butterfly models (D_{model}) from an avian UVS and VS visual perspective.

Table S2. Relative discriminability of model-mimic pairs (D_{mimic}) from avian UVS and VS visual systems in *eucharis, chrysippus* and *hector* mimicry rings.

Table S3. Relative discriminability of butterfly models and mimics (D_{mimic}) in the *genutia* mimicry ring.

Table S4. Relative discriminability of butterfly models and mimics (D_{mimic}) in the *Pachliopta* mimicry ring from an avian UVS and VS visual systems.

Table S5. Relative discriminability of butterfly models and mimics (D_{mimic}) in the *Euploea* mimicry ring from an avian UVS and VS visual systems.

Table S6. Relative discriminability of butterfly models and mimics (D_{mimic}) in the *Tirumala* mimicry ring from avian UVS and VS visual systems.

Figure S1. Butterfly mimicry rings in the Western Ghats.

Figure S2. Reflectance spectra of butterfly models and mimics in the Western Ghats.

Figure S3. Histograms showing the range and frequency of relative discriminability values (i.e., mimetic resemblance) for dorsal (white) and ventral (grey) wing coloration of butterfly mimics from an avian UVS and VS visual systems.