

# Mimicry and masquerade from the avian visual perspective

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**Abstract** Several of the most celebrated examples of visual mimicry, like mimetic eggs laid by avian brood parasites and palatable insects mimicking distasteful ones, involve signals directed at the eyes of birds. Despite this, studies of mimicry from the avian visual perspective have been rare, particularly with regard to defensive mimicry and masquerade. Defensive visual mimicry, which includes Batesian and Müllerian mimicry, occurs when organisms share a visual signal that functions to deter predators. Masquerade occurs when an organism mimics an inedible or uninteresting object, such as a leaf, stick, or pebble. In this paper, I present five case studies covering diverse examples of defensive mimicry and masquerade as seen by birds. The best-known cases of defensive visual mimicry typically come from insect prey, but birds themselves can exhibit defensive visual mimicry in an attempt to escape mobbing or dissuade avian predators. Using examples of defensive visual mimicry by both insects and birds, I show how quantitative models of avian color, luminance, and pattern vision can be used to enhance our understanding of mimicry in many systems and produce new hypotheses about the evolution and diversity of signals. Overall, I investigate examples of Batesian mimicry (1 and 2), Müllerian mimicry (3 and 4), and masquerade (5) as follows: 1) Polymorphic mimicry in African mocker swallowtail butterflies; 2) Cuckoos mimicking sparrowhawks; 3) Mimicry rings in Neotropical butterflies; 4) Plumage mimicry in toxic pitohuis; and 5) Dead leaf-mimicking butterflies and mantids [*Current Zoology* 58 (4): 630–648, 2012].

**Keywords** Mimicry, Masquerade, Protective coloration, Avian vision, Pattern, Luminance

## 1 Introduction

“Perfectly staggering” is how Henry Walter Bates (1862) first described the visual mimicry he observed in the Amazon when he formulated his influential ideas about mimicry in the animal kingdom. Now 150 years later, we are still mesmerized by rich examples of visual mimicry in the natural world. Recent years have seen huge advances in our understanding of signal processing and sensory ecology, particularly in terms of animal vision. As a result, it is now possible to evaluate visual mimicry from the perspective of the relevant signal receiver, which in many cases is a bird. Models of avian vision are now well described and many techniques for the study of color, luminance, and pattern from the avian visual perspective are readily available, making this a compelling time to investigate mimicry from a bird’s-eye view. Given the vast and growing interest in research on coloration, this is an opportune moment to integrate sensory ecology into broad questions about the evolution of signals.

Visual mimicry is relevant to birds in a wide variety of contexts, as birds are frequent victims of both aggressive and defensive mimicry. Broadly speaking, vis-

ual mimicry occurs when the visual similarity of one species (the mimic) to another (the model) confers protection to one or both parties. Aggressive mimicry occurs when predators or parasites mimic a harmless or beneficial model to fool their victims. In contrast to aggressive mimicry, defensive mimicry occurs when prey organisms share a visual signal that functions to deter predators (Wallace, 1889; Poulton, 1890). Batesian mimicry occurs when a palatable or harmless species mimics an unprofitable model, such as a harmless hoverfly mimicking a dangerous wasp. Müllerian mimicry occurs when two or more unpalatable species share a warning signal and together shoulder the burden of educating naïve or forgetful predators (Ruxton et al., 2004). The most notable example of Müllerian mimicry is the resemblance among many species of unpalatable Neotropical butterflies, which occupy a number of mimicry rings throughout South America. Related to defensive mimicry is masquerade, a form of camouflage that prevents recognition and promotes misclassification. Masquerade occurs when an organism evades predator recognition by resembling an inedible and unexciting object such as a leaf, pebble, stick, or bird dropping (Skelhorn et al., 2010a).

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Visual mimicry involves signal senders and signal receivers, with the type of signal often influenced by the receiver's sensory ecology (Joron, 2003). It is therefore essential to investigate mimicry from the perspective of the appropriate receiver, which in many cases is a bird. Despite this, few studies of mimicry have considered the bird perspective; traditional approaches have relied instead on human vision, which lacks many important features of avian perception. Birds have one of the most sophisticated visual systems of any vertebrate (Goldsmith, 1990; Goldsmith, 2006). Compared to trichromatic humans, tetrachromatic birds have a fourth color cone that is sensitive to ultraviolet wavelengths. Birds also have cone oil droplets with carotenoid filters (in the short, medium, and long wavelength-sensitive cones) that help to refine spectral sensitivities, as well as a class of double cones believed to encode luminance (brightness) vision (Jones and Osorio, 2004; Cuthill, 2006). In recent years, the widespread availability of spectrophotometers and digital cameras, coupled with new visual models and tools, has rapidly changed the way we measure and analyze color (Bennett and Théry, 2007; Stevens, 2011).

In contrast to the growing body of research exploring a bird's-eye view of aggressive mimicry (Safran and Vitousek, 2008), very few studies investigating defensive mimicry have accounted for the avian visual perspective. This is surprising given how much progress has been made in terms of understanding predator perception and prey defenses with respect to camouflage (Théry and Gomez, 2010; Stevens and Merilaita, 2011), yet little of this has been applied to studies of defensive mimicry *per se*. A notable exception is recent work by Bybee et al. (2012), in which the authors modeled mimetic yellow wing coloration of Heliconiini tribe butterflies from the perspective of both butterfly and bird observers.

In this paper, I argue that the focus of mimicry research should shift toward a mechanistic understanding of how predator sensory systems have influenced the evolution of mimetic signals. Specifically, I address a number of questions about mimicry and masquerade that can only be answered using sensory ecology. Are mimics constrained in their ability to match their models' colors? What patches of a pattern are most important for mimicry? How strongly have mimics converged on a shared warning pattern? How well do masqueraders match the colors of uninteresting natural objects? My aim is to demonstrate the broad potential held by integrating models of avian vision into studies of Bate-

sian mimicry, Müllerian mimicry, and masquerade.

Here, I present five case studies covering diverse examples of defensive mimicry and masquerade as seen by birds. The best-known examples of defensive visual mimicry typically come from the invertebrate world (Poulton, 1890; Théry and Gomez, 2010), and three of the case studies presented here focus on classic examples of visual mimicry by insect prey. Birds themselves can also exhibit defensive visual mimicry in an effort to escape mobbing or deter larger avian predators, though examples of this are rare (Negro, 2008; Sazima, 2010). Two of the case studies here focus on putative examples of plumage mimicry by birds. Overall, I investigate examples of Batesian mimicry (1 and 2), Müllerian mimicry (3 and 4), and masquerade (5) as follows: 1) Polymorphic mimicry in African mocker swallowtail butterflies; 2) Cuckoos mimicking sparrowhawks; 3) Mimicry rings in Neotropical butterflies; 4) Plumage mimicry in toxic pitohuis; and 5) Dead leaf-mimicking butterflies and mantids. I chose these systems not just for their fascinating natural history but also for their ability to highlight key questions in sensory ecology and generate new predictions about the evolution of visual signals.

## 2 Avian vision: Background and visual models

In this section, I provide a brief overview of bird vision and introduce the most common techniques for quantifying bird color and pattern. For modeling color, color space analyses and receptor noise-discrimination models are the most common techniques. For quantifying pattern, specific models of luminance perception can be combined with spatial information from calibrated images. For a recent review, see Stevens (2011).

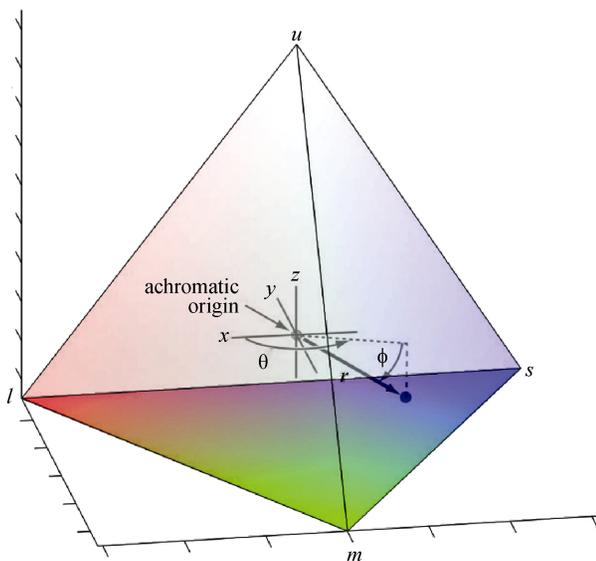
### 2.1 Color

Birds have four single cone-types that are sensitive to longwave (l), mediumwave (m), shortwave (s), and ultraviolet (u) or violet (v) light. As tetrachromats (four color cone-types), birds can likely distinguish many colors that trichromatic (three color cone-types) humans cannot (Cuthill, 2006). Diurnal birds fall into one of two classes of color vision (ultraviolet-sensitive UVS or violet-sensitive VS) depending on the sensitivity of their fourth cone to ultraviolet light (Ödeen and Hastad, 2003). Microspectrophotometry sampling of a range of avian species (Hart, 2001b) and well-established phylogenetic estimates of avian color vision (Ödeen and Hastad, 2003) indicate that VS vision is the ancestral

condition in birds and that UVS vision has evolved independently many times; recent evidence indicates that color vision has changed between UVS and VS at least eight times in passerines alone (Ödeen et al., 2011). Apart from differences between the UVS and VS classes, birds appear to have relatively fixed spectral sensitivities (Osorio and Vorobyev, 2008). The presence of oil droplets with carotenoid filters can help to fine-tune the spectral sensitivities of the shortwave, mediumwave, and longwave cones, thereby reducing spectral overlap and increasing the number of colors birds can see and discriminate (Goldsmith, 1990; Vorobyev et al., 1998; Vorobyev, 2003). Opponent mechanisms (Osorio et al., 1999) and color categorization (Osorio, 2009) likely play important roles in avian vision, though still little about these features is understood in birds (Kelber and Osorio, 2010). For detailed reviews on avian color perception, see Kelber et al., 2003; Endler and Mielke, 2005; Cuthill, 2006; Osorio and Vorobyev, 2008.

#### Avian tetrahedral color space modeling

Avian tetrahedral color spaces (Fig. 1) provide a straightforward and parsimonious way to quantify color variation (Goldsmith, 1990; Endler and Mielke, 2005; Stoddard and Prum, 2008). The avian tetrahedral color space is a chromaticity diagram in which the achromatic dimension has been removed and only the chromatic



**Fig. 1** A tetrahedral avian color space (from Stoddard and Prum, 2008)

The position of a color point is determined by the relative stimulation of the ultraviolet or violet ( $uv/v$ ), blue ( $s$ ), green ( $m$ ), and red ( $l$ ) retinal cones. The center of the tetrahedron is the achromatic point. A color point is defined by  $\theta$ ,  $\phi$ , and  $r$ ; where hue is defined by the angles  $\theta$  and  $\phi$  and saturation is given by the magnitude of  $r$ .

signal is considered. In many vertebrates, achromatic and chromatic perception are widely believed to be independent processes (Kelber and Osorio, 2010; but see Lind and Kelber, 2011). In this paper, I model avian perception of color in tetrahedral color space (Stoddard and Prum, 2008; 2011) using the free shareware computer program TETRACOLORSPACE for MATLAB 7 software (program is available from the author).

The idealized stimulus,  $Q_i$ , of each color cone-type is estimated by the reflectance spectrum of a plumage patch:

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

where  $R(\lambda)$  is the reflectance spectrum of the plumage patch, and  $C_r(\lambda)$  is the spectral sensitivity function of each cone type  $r$ .  $R(\lambda)$  and  $C_r(\lambda)$  functions are normalized to have integrals of 1, and constant illumination is assumed across all visible wavelengths (Stoddard and Prum, 2008). For each color, the idealized stimulation values of the four color cones –  $Q_i$  – are normalized to sum to one, yielding relative  $[uv/v \ s \ m \ l]$  values. The  $[uv/v \ s \ m \ l]$  values of each reflectance spectrum are transformed to a color point with spherical coordinates  $\theta$ ,  $\phi$ , and  $r$ , which define a color vector in the tetrahedral color space. This tetrahedral geometry places the achromatic point of equal cone stimulation – white, black, or gray – at the origin and the  $uv/v$  vertex along the vertical  $z$ -axis. Each color has a hue and saturation. Hue is defined as the direction of the color vector, given by the angles  $\theta$  and  $\phi$  which are analogous to the longitude and latitude, respectively. Saturation, or chroma, is given by the magnitude of  $r$ , or its distance from the achromatic origin.

#### Receptor noise-limited discrimination modeling

For calculating threshold differences between colors, which is often important when judging how closely one color mimics another, the Vorobyev-Osorio (1998) receptor noise-limited discrimination model can be used. The model assumes that discrimination is coded by opponent mechanisms and that their performance is limited by receptor noise. For full details on the model, see Vorobyev-Osorio (1998) and Kelber et al. (2003). The model output is in perceptual units called Just-Noticeable Differences, where values less than 1 indicate that two colors are perceptually identical and values greater than 1 indicate that the two colors are perceptually distinct.

## 2.2 Luminance and pattern perception

In birds, perception of pattern and texture is believed

to be a function of luminance (achromatic) vision. Luminance is probably encoded by double cones (Jones and Osorio, 2004; Osorio and Vorobyev, 2005), which comprise about 50% of cones in the avian retina (Hart and Hunt, 2007). Luminance-based spatial vision in birds and other vertebrates involves breaking down information in a two-dimensional scene and processing it at different spatial frequencies. At each different scale, receptive fields of different sizes and orientations are tuned to different spatial information (Bruce et al., 2003; Troscianko et al., 2009), allowing the visual system to extract meaningful pattern and texture information from the scene.

#### *Luminance vision and pattern modeling*

To analyze the pattern sizes and contrasts of animal markings, one approach is to use granularity analysis. This method has been used to quantify pattern differences in cuttlefish camouflage body patterns (Barbosa et al., 2008; Chiao et al., 2009) and pigmentation patterns on eggshells (Stoddard and Stevens, 2010; Spottiswoode and Stevens, 2010). The first step is to obtain digital images and convert them to bird luminance (see *Materials and Methods*). Most animal markings comprise light and dark components with various shapes, orientation, and texture, with some markings more fine-grained than others; many of these differences can be captured by evaluating the image at different spatial scales (Chiao et al., 2009). This is achieved by performing a fast Fourier transform, which applies several band-pass filters to the original image to produce a set of new images containing information at different spatial scales. Real visual systems do not break down information in exactly the same way that a Fourier transform does, but low-pass spatial filtering in the early stages of visual processing does appear to be a common feature of vertebrate vision (Godfrey et al., 1987). Ultimately, a ‘granularity spectrum’ can be produced from the filtered images. The spectrum provides information about overall pattern contrast and the relative contribution of different-sized markings. For full details, see Stoddard and Stevens, 2010.

### 3 Materials and Methods

A number of approaches exist to collect and analyze color and pattern data. Reflectance spectrophotometry is a widely used technique for capturing the reflectance of a color over a range of wavelengths (Andersson and Prager, 2006). One major drawback to spectrophotometry is that it does not capture the spatial structure of scenes. For this reason, digital photography provides a

powerful alternative – if used appropriately (see Stevens et al. 2007) – because it allows color and pattern information to be captured together. In this paper, I have used both approaches and I summarize them briefly here.

#### 3.1 Reflectance spectrophotometry

Using the collections of the University Museum of Zoology, Cambridge (UMZC), I obtained reflectance spectra from a number of butterfly Lepidoptera and mantid Mantidae specimens. These included several polymorphic *Papilio dardanus* females, including *P. d. meriones*, *P. d. hippocoonides*, *P. d. trophonius*, *P. d. planemoides*, *P. d. cenea*, *P. d. hippocoon*, as well as the butterflies they mimic, including *P. d. meriones* (male), *Amauris niavius niavius*, *Danaus dorripus*, *Planema poggei*, *Amauris echeria jacksoni*, and *Amauris dominicanus*. All visually distinct (to human eyes) color patches on each of the dorsal forewings and hindwings were measured on one specimen per race or species. Additionally, I measured colors on the ventral side of 8 dead leaf-mimicking butterflies (*Kallima spp.*) and on the dorsal side of 4 dead leaf mantids *Deroplatys truncata* and 4 giant dead leaf mantids *Deroplatys desiccata*. To compare the dead leaf-mimicking butterflies and mantids to natural dead leaves, I obtained reflectance spectra from the front and back of 45 dead leaves representing a diverse range of plant species in the Cambridge University Botanic Garden (Cambridge, UK).

Using the collections of the Natural History Museum (Tring, UK), I obtained reflectance spectra of plumage patches on 6 (2 male, 2 female, 2 juvenile male) common cuckoo *Cuculus canorus* specimens and 4 (2 male, 2 female) sparrowhawk *Accipiter nisus* specimens. Spectra were averaged to obtain one spectra per patch per sex. I also measured plumage patch reflectance of several birds in the genus *Pitohui*, including 3 hooded pitohui *Pitohui dichlorus* specimens and 11 variable pitohui *Pitohui kirhocephalus* specimens representing a number of subspecies, including *P. k. meridionalis* (2), *P. k. nigripectus* (2), *P. k. dohertyi* (3), *P. k. aruensis* (2), and *P. k. uropygiali* (2). Reflectance spectra were measured from 6 standard plumage patches: crown, back, rump, throat, breast and belly. Additional distinct color patches were measured if they were visible to the human eye. For most species, reflectance spectra were measured once per patch per individual; however for several specimens, multiple reflectance spectra were measured per patch to ensure that measurements were repeatable.

All color measurements were obtained using an Ocean Optics USB2000 spectrophotometer with a PX-2

pulsed xenon light source and an R400-7-UV/VIS reflectance probe (Ocean Optics Inc., Dunedin, FL, USA), using a Spectralon 99% white reflectance standard as a reference. All measurements were taken at a fixed distance (5 mm) and angle (45°) from the specimen using a slanted plastic sleeve attached to the end of the probe. Extra caution should be taken when measuring iridescent colors (Meadows et al., 2011); however, none of the bird or butterfly colors measured were highly iridescent.

To perform visual modeling of reflectance spectra, I used representative VS and UVS avian spectral sensitivities as follows: 1) African mocker swallowtail butterflies: standard VS and UVS cone-types (Endler and Mielke, 2005), representative of diverse avian predators (Turner, 2005); 2) cuckoos and sparrowhawks: blue tit *Cyanistes caeruleus* UVS cone-type (Hart et al., 2000), representative of passerine host species (Stoddard and Stevens, 2011); 3) Neotropical butterflies: see next section; 4) pitohuis: standard VS cone-type (Endler and Mielke, 2005) with relative proportions of cone-types in the retina for peafowl *Pavo cristatus* (Hart, 2001a), representative of VS avian predators like raptors (Ödeen and Hastad, 2003); 5) dead leaf-mimics: standard VS and UVS cone-types (Endler and Mielke, 2005), representative of diverse avian predators. VS and UVS modeling in case studies 1 and 5 yielded qualitatively similar results, so only VS results are presented.

### 3.2 Digital photography

Using the collections of the University Museum of Zoology, Cambridge (UMZC), I obtained digital images of Neotropical butterfly species involved in five different mimicry rings and sub-rings: **melanic tiger**: *Eresia pelonia ithomiola*, *Hypscada anchiala fallax*, *Mechanitis* sp.; **tiger sub-ring**: *Ceratinia* sp., *Mechanitis lysimnia*, *Placidula euryanassa*; **tiger sub-ring**: *Dismorphia amphione praxinoe*, *Heliconius ismenius telchinia*, *Mechanitis menapis saturata*; **tiger sub-ring**: *Hypothyris lycaste dionaea*, *Mechanitis menapis doryssus*; *Mechanitis mazaesus fallax*; **large transparents**: *Patia orise*, *Eutresis hypereia imitatrix*, *Methona confusa*.

Images were taken using a Fujifilm IS Pro ultraviolet (UV)-sensitive digital camera with a quartz CoastalOpt UV lens (Coastal Optical Systems). A UV- and infrared (IR)-blocking filter was used to obtain images in the human visible range and a UV pass filter was used for UV images. All images included a Spectralon gray reflectance standard (Labsphere, Congleton, UK). Images

were taken at a fixed distance and angle from all specimens. All images were linearized with respect to light intensity (Stevens et al., 2007). Because pattern and not color was of principal interest, images were calculated based on the luminance channel encoded by double cones (Jones and Osorio, 2004; Osorio and Vorobyev, 2005). Images were transformed from camera color space to bird color space by relating the camera spectral sensitivity to the sensitivity of a bird's double cones (Fig. 2), using in this case the spectral sensitivity of a European starling *Sturnus vulgaris* (Hart et al., 1998), which has UVS vision. Starlings are occasional butterfly predators (Sakai, 1994) and their UVS visual system is likely to be representative of diverse avian predators in the Neotropics. For full details, see Stoddard and Stevens (2010). For each butterfly image, a square region of interest was cropped from the area containing the left dorsal forewing and hindwing; this image was used in the pattern analysis (see *Luminance vision and pattern modeling*).

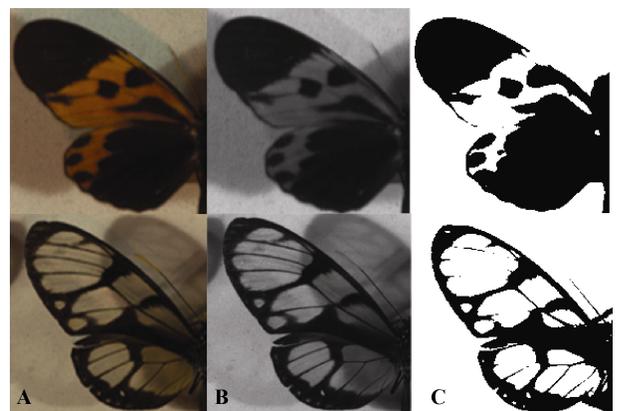


Fig. 2 (A) Normal color images of butterfly wings are mapped to (B) a starling's luminance channels and (C) can be subsequently thresholded to quantify the degree of pattern coverage.

Photo credit: M. C. Stoddard.

## 4 Case studies

### Batesian mimicry

#### 4.1 Polymorphic mimicry in African mocker swallowtail butterflies

*African mocker swallowtails provide one of the best examples of polymorphic, sex-limited Batesian mimicry. Here I use an avian tetrahedral color space model to test the hypothesis that female swallowtails are constrained in their ability to match the range of colors exhibited by their toxic models.*

The African mocker swallowtail *Papilio dardanus*, which E. B. Poulton (1924) called “the most interesting

butterfly in the world,” represents one of the best examples of mimetic polymorphism in nature. Mimetic polymorphism often arises in Batesian mimicry complexes; since the mimic’s survival is increased if it is rare relative to the model, frequency-dependent selection on mimics can lead to polymorphisms (Ruxton et al., 2004). While *P. dardanus* males are generally monomorphic, palatable females mimic several different toxic models (often in the family Danaidae) throughout their range in sub-Saharan Africa and are often polymorphic in a single geographic area (Vane-Wright et al., 1999). Some of the female morphs are andromorphic mimics of *P. dardanus* males, a tactic that may increase predation risk (mimicking males offers no Batesian protection) but reduce male aggression (Cook et al., 1994). Batesian mimicry is often restricted to one sex, and in butterflies it is almost always the female that exhibits mimicry. The most popular explanations for this are that females may be more vulnerable to predation than males or that sexual selection conserves male but not female appearance (via female mate choice or male-male competition) (Ruxton et al., 2004).

Because *P. dardanus* female morphs belong to one species yet mimic many different toxic species, *P. dardanus* females could be physiologically constrained in their ability to reproduce all colors of their toxic models. In other words, it might be possible for toxic models to create colors that are challenging for *P. dardanus* females to match. Does this appear to be the case? Side-by-side comparison of female morphs (Fig. 3A) to their toxic models (Fig. 3B) reveals that the color distributions in avian color space (Fig. 3C, D) are very similar, suggesting that, to a bird’s eye, the mimics’ colors are indeed a good match to those of the models (Fig. 3). To investigate this further, we can compare the gamut, or full range, of colors occupied by all *P. dardanus* female morphs collectively (Fig. 3A) to the color gamut of all of their models (Fig. 3B). (Note that *P.d. meriones* female and male representatives [Fig. 3, top row] were excluded from this analysis because they are the same species). The female mimics collectively occupy 0.11% of avian color space, compared to 0.22% by the models; the small volumes are a consequence of the linear distribution of colors in both groups. Given the small sample size used here, it would be hazardous to draw conclusions from this. Still, the fact that *P. dardanus* mimics appear to achieve slightly reduced color diversity relative to their models invites further investigation, particularly because *Papilio* butterflies may have a slightly different set of color-producing pigments with

which to work; for instance, yellow papiliochrome pigments are unique to Papilionidae (Koch et al., 2000). In sum, *P. dardanus* females appear to be very close mimics of their models, but there could be physiological constraints that keep *P. dardanus* from evolving a perfect color match to all models. It should be noted that in full-fledged studies “close mimic” or “perfect color match” should be properly qualified; ideally, a balanced analysis would compare not only mimics to models but also mimics to non-models in the same locality. This would establish a baseline ‘null hypothesis’ against which the degree of color mimicry could be rigorously compared. Additionally, it is difficult to demonstrate conclusively that a lack of close mimicry stems from physiological constraints rather than from a lack of selection pressure or evolutionary lag. However, visual modeling has yielded insights into physical constraints on the evolution of colorful signals in birds (Stoddard and Prum, 2011) and could, on a larger scale, reveal similar limitations in butterflies.

Using a sensory ecology framework to investigate *P. dardanus* mimicry can provoke a number of important biological questions. How good does mimicry have to be in order for birds to confuse the mimics with models? Perhaps this could be tested in the field using computer-generated butterfly-like targets, each colored in a way that, to a bird’s eye, increasingly deviates from the model (e.g., Cuthill et al., 2005). From a physiological standpoint, have the mimics evolved special chemical pigments to achieve better mimicry? What genes are involved? In *P. dardanus*, we are rapidly learning more about the genetic architecture underlying mimicry (Beldade and Brakefield 2002), which is apparently controlled by a single supergene locus responsible for coordinated differences in wing pattern, shape, and color (Nijhout, 2003; Clark et al., 2008). By combining this rich genetic information with visual modeling, we can start to understand *P. dardanus* mimicry in terms of both its mechanism and function.

#### 4.2 Cuckoos mimicking sparrowhawks: a sheep in wolf’s clothing

*A longstanding hypothesis predicts that common cuckoos, which sneak their eggs into the nests of host birds, mimic dangerous sparrowhawks to reduce mobbing by hosts. Here I use models of avian color vision to investigate how closely cuckoo and sparrowhawk plumage patches match to determine which patches may be most important for effective color mimicry.*

Wallace (1889) recognized that cases of mimicry by birds were rare but existent, highlighting examples



**Fig. 3** Polymorphic Batesian mimicry in African mocker swallowtail *Papilio dardanus* butterflies

Palatable females (column A) mimic several different toxic models (column B, except *P. dardanus meriones*) throughout their range in sub-Saharan Africa. Some female morphs are andromorphic mimics of *P. dardanus* males (e.g., *P. dardanus meriones*, top row, column B). Mimicking undefended males offers no Batesian protection but may reduce male aggression directed toward females. Colors of *P. dardanus* mimics (column C) are mapped in avian tetrahedral color space alongside colors of their respective models (column D). Each color patch on the butterfly is represented as point in color space, with its position based on how it would stimulate the four bird color cone-types. Modeling was done using VS cone-type sensitivities. Coloration of the tetrahedra is representative. Photos are copyright UMZC and taken by M. C. Stoddard.

“presented by several species of cuckoos, an exceedingly weak and defenceless group of birds...Our own cuckoo is, in colour and markings, very like a sparrow-hawk.” Recent work supports the idea that common cuckoos *Cuculus canorus* are Batesian mimics of dangerous sparrowhawk *Accipiter nisus* predators (Davies

and Welbergen, 2008; Welbergen and Davies, 2011). Note that this type of mimicry can be considered Batesian because cuckoos, which can be safely approached by hosts, mimic a dangerous model, but it can also accurately be described as aggressive because ultimately hawk-mimicry allows cuckoos to gain access to hosts

and exploit their reproductive investment (see Welbergen and Davies, 2011).

Reed warblers *Acrocephalus scirpaceus*, a favorite host of the common cuckoo, often defend themselves against cuckoo parasitism by aggressively mobbing cuckoos that approach the nest (Welbergen and Davies, 2009), sometimes inciting neighbors to join in the attack or increase mobbing behavior at their own nests (Davies and Welbergen, 2009). To evade mobbing, cuckoos may gain a protective advantage by mimicking the appearance of deadly sparrowhawks; this discourages reed warbler hosts from approaching lest they make a fatal mistake (Welbergen and Davies, 2011). Cuckoos and

sparrowhawks generally resemble one another in terms of body size and shape, flight behavior, and plumage (Fig. 4), which typically comprises gray or brown upperparts and pale barred underparts (Welbergen and Davies, 2011). In a field experiment, Welbergen and Davies (2011) demonstrated that reed warblers are less likely to approach taxidermy cuckoos with hawk-like barred plumage than taxidermy cuckoos manipulated to have non-barréd plumage, indicating that some aspects of hawk mimicry effectively reduce host mobbing. This experiment explored aspects of plumage pattern mimicry (*i.e.*, presence of barring), but plumage color mimicry has not yet been studied.



**Fig. 4 Batesian mimicry in birds**

Common cuckoos *Cuculus canorus* (male, left) may gain a protective advantage by mimicking dangerous sparrowhawks *Accipiter nisus* (male, right). Note that this type of mimicry can also be considered aggressive mimicry (see text for details). Photo credits: D. Kjaer.

How closely, to a host bird's eye, do common cuckoo plumage colors resemble those of sparrowhawks, and what does this reveal about the importance of certain colors or patches for mimicry? Table 1 shows color differences (given in Just-Noticeable Differences) between plumage patches on cuckoos (male, female, and juvenile) and sparrowhawks (male, female) from the perspective of a blue tit, which has UVS vision representative of many passerine host birds. JND values less than 1.00 indicate that two colors are indiscriminable, with values less than 3.00 (Siddiqi et al., 2004; Cassey et al., 2009) believed to be difficult to distinguish under decent light conditions. Color comparisons are shown in bold (Table 1) if two colors are separated by fewer than 3.00 JNDs, indicating a good match. Above threshold values, JNDs can become difficult to interpret because they may not be proportional to minimum threshold distances, particularly if color categorization is involved (Vorobyev and Osorio, 1998; Vorobyev et al., 2001; Ham and

Osorio, 2007).

With the caveat that sample sizes were small (2 individuals per sex per species), two preliminary observations can be made. First, the crown, rump, back, and belly appear to be important for mimicry, especially in adult cuckoos, while a mimetic throat, breast, or nape may be less essential. The gray-brown plumage of male and female common cuckoos on the crown, back, and rump and white plumage on the belly are a good match to corresponding color patches on sparrowhawk males. The rufous-colored crown, back, and rump of juvenile male cuckoos are a poor match to those of sparrowhawk males, although dark and light patches on the breast and white belly provide a better match. A second observation is that female and juvenile male cuckoos appear to be a better match to sparrowhawk females than are cuckoo males. Overall, cuckoo males match sparrowhawks only in a few patches (5 matches in all), while female cuckoos match sparrowhawks better (10

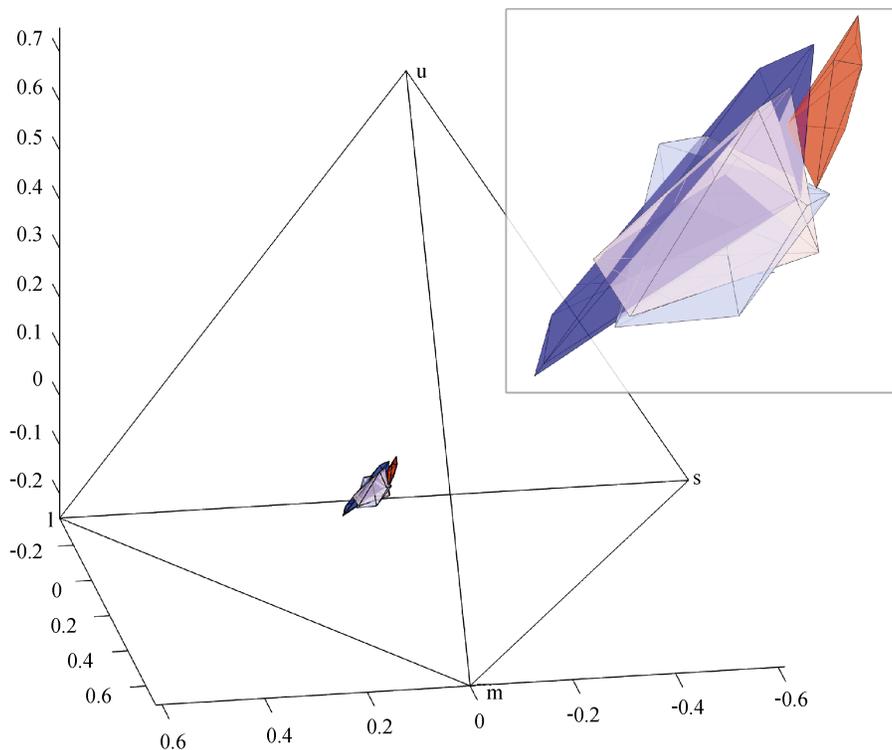
matches in all); juvenile males also achieve a good match (10 matches in all). Modeling in avian color space (Fig. 5) illustrates that, in this small-scale comparison, female cuckoos achieve a better match to sparrowhawk colors than do male cuckoos. Fig. 5 shows the distribu-

tions of color patches on a male cuckoo (red), female cuckoo (pink), male sparrowhawk (blue), and female sparrowhawk (light blue). The overlap between the female cuckoo and the male and female sparrowhawks is pronounced, while the male cuckoo colors fall just

**Table 1** Just-Noticeable Differences between plumage color patches on cuckoos and sparrowhawks

	<i>Cuculus canorus</i> (male)	<i>Cuculus canorus</i> (female)	<i>Cuculus canorus</i> (juvenile male)	
crown	<b>2.7</b>	<b>1.7</b>	6.7 (l), 6.4 (d)	
back	<b>1.9</b>	<b>1</b>	9.2 (l), 6.7 (d)	
rump	<b>1.3</b>	<b>1.1</b>	5.3	
throat	10.3	4.1	7.4 (l), 3.9 (d)	
breast (dark)	11.3	4.3	<b>2</b>	<i>Accipiter nisus</i> (male)
breast	3.6	5.3	<b>2.4</b>	
belly (dark)	7.6	5.7	3.1	
belly	<b>0.4</b>	<b>1.7</b>	<b>3</b>	
crown	5.9	<b>1.6</b>	3.4 (l), 3.2 (d)	
back	4.7	<b>2.5</b>	6.3 (l), 3.9 (d)	
rump	4.7	<b>2.3</b>	<b>2</b>	
throat	5.9	<b>1.6</b>	<b>2.9 (l), 4.1 (d)</b>	
breast (dark)	6.8	<b>0.7</b>	<b>3</b>	<i>Accipiter nisus</i> (female)
breast	3.8	5.3	<b>2.3</b>	
belly (dark)	7	5.1	<b>2.9</b>	
belly	<b>1.8</b>	<b>0.9</b>	<b>1.7</b>	
nape		5.9	<b>0.4</b>	

Boxes with JND  $\leq 3$  are shown in bold, indicating that colors are very similar. Visual modeling was done from the perspective of a blue tit (UVS cone-type). Some patches consisted of both light (*l*) and dark (*d*) plumage, both of which were measured.



**Fig. 5** Plumage mimicry in avian color space

Avian color space modeling suggests that female cuckoos, whose plumage color patches are represented by the pink polyhedron, may be a slightly better match to male (dark blue) and female (light blue) sparrowhawk plumage colors, compared to male cuckoos (red polyhedron), whose patch colors fall largely outside the region of overlap. Modeling was done using UVS cone-type sensitivities representative of a host bird.

outside this region of overlap. Without a more comprehensive experimental design, these observations are interesting but inconclusive. To properly test the hypothesis that female cuckoos are a better match than male cuckoos to sparrowhawks, cuckoo colors should be compared to a null distribution of feathers from diverse avian taxa. Only then could one test whether females and/or males are actually more similar to sparrowhawks than would be expected by chance.

If a fully developed study with appropriate baseline comparisons were to demonstrate that female cuckoos achieve a better color match than males to sparrowhawks, this might be explained by the fact that females, not males and juveniles, must get close to host nests in order to lay their eggs. Thus, females have the most to gain by mimicking hawks and evading mobbing. However, hawk resemblance might also benefit males and juveniles if it helps to reduce mobbing in the general vicinity, limit attacks by hawks, or enhance camouflage (Welbergen and Davies, 2011). Ultimately, it would be fruitful to combine color modeling with methods for studying barred plumage (Gluckman and Cardoso, 2010) in an effort to determine which visual cues might be most salient to hosts trying to distinguish between a cuckoo and hawk (Trnka and Prokop, 2011).

## Müllerian mimicry

### 4.3 Mimicry rings in Neotropical butterflies

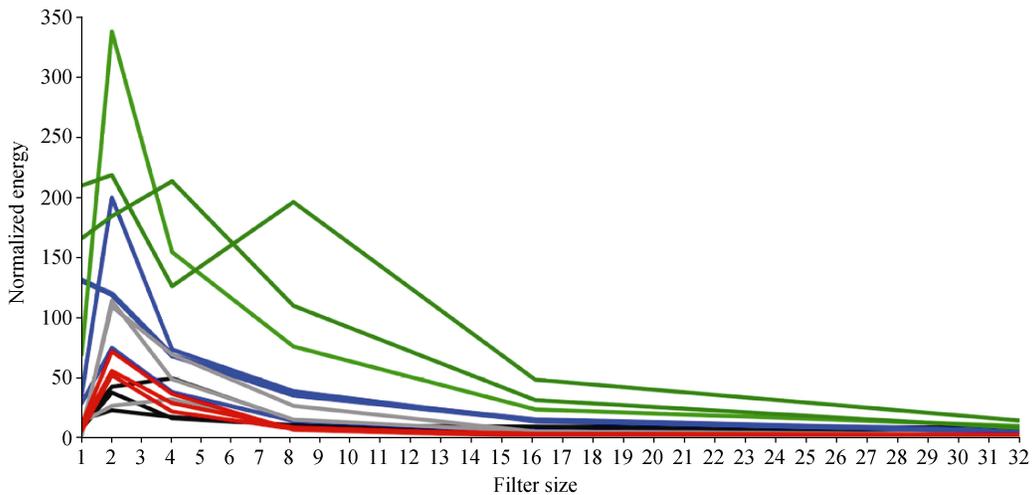
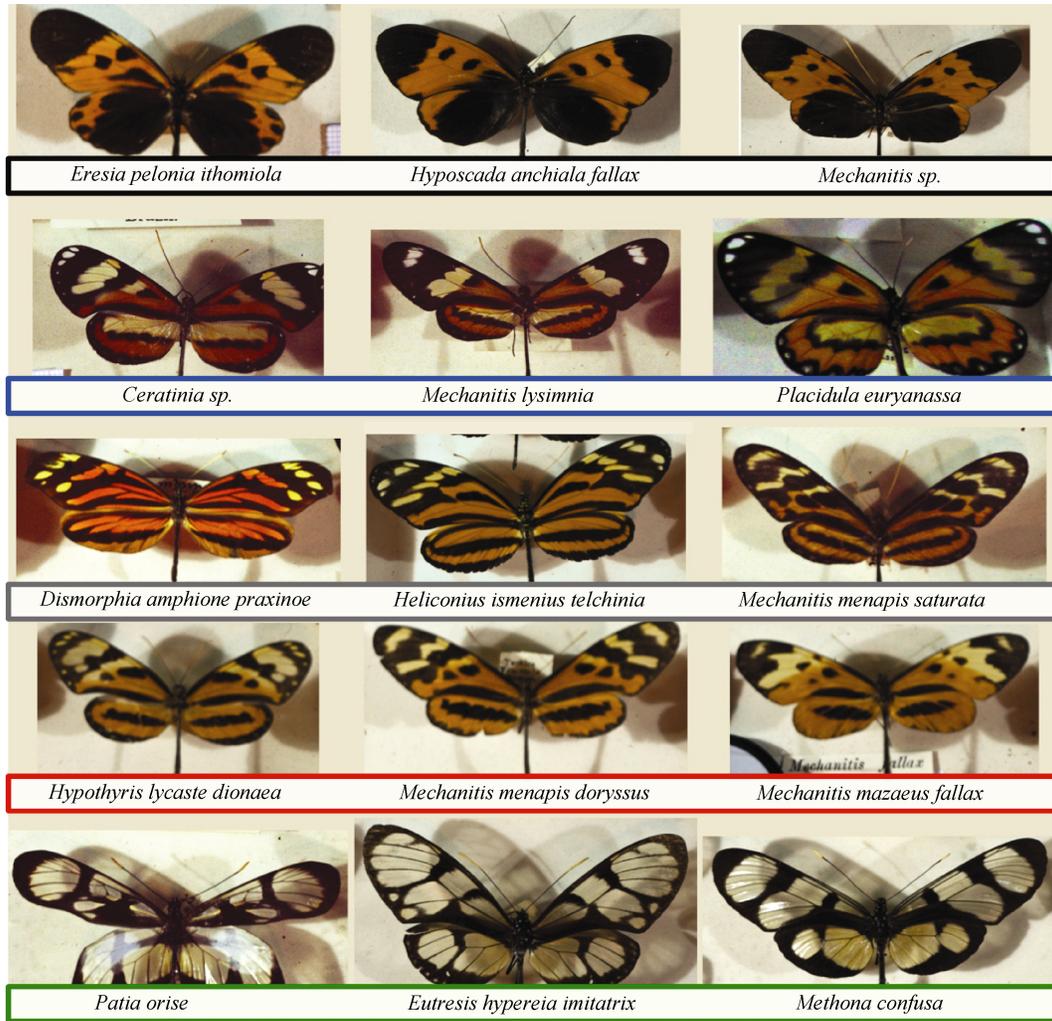
*The resemblance among distasteful Neotropical butterflies in South America is a quintessential example of Müllerian mimicry. Many unpalatable butterfly species belong to mimicry rings, which are assemblages of species that share the same warning pattern. In this explorative study, I combine a model of avian luminance vision with objective pattern analysis to determine whether convergence on a shared warning pattern is stronger in some mimicry rings than in others. I then use these results to generate predictions.*

A number of Müllerian mimicry rings can exist in a single geographic area, and rings often exhibit geographic variation across a wide range (Mallet and Gilbert, 1995; Turner, 2005). Neotropical mimicry rings often include unpalatable species in the Ithomiinae, Danainae, and Heliconiinae subfamilies, and occasionally palatable Dismorphiinae species as well (Mallet and Gilbert, 1995). The relationships between species participating in these mimicry rings are often extremely complex, and readers should consult in-depth reviews (Mallet and Gilbert, 1995; Joron, 2003; Ruxton et al., 2004; Turner, 2005) for detailed information.

Although polymorphisms can exist within a Müllerian mimicry ring (see Ruxton et al., 2004), in general the expectation is that participants in a given ring should converge on a single shared warning color pattern. A recent empirical study by Pinheiro (2003) showed that tropical kingbirds *Tyrannus melancholicus* and cliff flycatchers *Hirundinea ferruginea* selectively avoided mimetic Neotropical butterflies (mimicry ring participants), particularly in habitats where birds had prior experience with unpalatable species. Clearly, it benefits butterflies to have the “right kind” of signal (Ruxton et al., 2004). What is the right kind of signal? In this case study, I ask: within a given mimicry ring, how closely do wing patterns mimic one another? Has convergence on the same pattern signal been stronger in some mimicry rings than others?

Almost without exception, mimicry rings have been characterized from the human visual perspective, but this can be dangerous given that avian predators may have different perceptual biases; in other words, birds might generalize more or less in certain directions, resulting in mimicry that appears very good to birds but poor to humans, or vice versa (Joron, 2003). Earlier (case studies 1 and 2) I showed how color vision modeling can be used to quantify the degree of color mimicry. Here I focus on pattern rather than color mimicry because patterning (*i.e.*, the spatial arrangement of markings) in mimicry rings appears to be at least as, if not more, variable than coloration *per se*.

Using digital images converted to luminance (for a UVS starling predator) and granularity analysis, I calculated the granularity spectra for three representatives each from five different mimicry rings and subrings located throughout South America, including the melanic tiger, tiger (various subrings), and large transparent rings (Fig. 6, and see Joron 2003 for details and nomenclature). The resulting pattern “fingerprints” provide information about pattern texture; the shape of the spectrum depends on the contribution of different-sized markings to the overall pattern (small filter sizes correspond to large markings, and large filter sizes correspond to small markings) and the amplitude of the spectrum depends on pattern contrast (higher amplitude corresponds to higher contrast between light and dark parts of the pattern). In general, similar patterns will have similar granularity spectra. Fig. 6 shows that butterfly pattern profiles closely cluster according to mimicry ring, suggesting that wing spatial patterns within a mimicry ring are both faithfully repeated within the ring and distinct from the patterns of other rings.



**Fig. 6 Müllerian mimicry rings in Neotropical butterflies**

Granularity spectra are shown for three representatives each from five different mimicry rings and subrings located throughout South America, including the melanic tiger (black lines), tiger (various subrings; blue, gray, red lines), and large transparent (green lines) rings. The resulting pattern profiles provide information about pattern texture; the shape of the spectrum depends on the contribution of different-sized markings to the overall pattern (small filter sizes correspond to large markings, and large filter sizes correspond to small markings) and the amplitude of the spectrum depends on pattern contrast (higher amplitude corresponds to higher contrast between light and dark parts of the pattern). Butterfly patterns closely cluster according to mimicry ring, suggesting that wing spatial patterns within a mimicry ring are both highly repeatable within the ring and distinct from the patterns in other rings. Note that pattern analyses were performed on images converted to luminance, though color images are shown here for clarity. Photos are copyright UMZC and taken by M. C. Stoddard.

Closer inspection shows that the wing patterns of some mimicry rings are less variable than others. For example, the three species in the tiger subring represented by the red lines (Fig. 6) have wing patterns that produce almost identical granularity spectra, while the three representatives of the large transparent mimicry ring (green lines) have more variable wing patterns. If this observation were to hold up to in-depth analysis, we might predict that convergence has been stronger in this particular tiger subring than in the large transparents. Perhaps selection by visual predators has acted in different ways on the different mimicry rings, or perhaps physiological constraints in the large transparents prevent close mimicry. Another possibility is that the number of Müllerian mimics participating in a ring influences the degree of mimicry. For instance, as more and more Müllerian mimics join a mimicry ring, predators may be forced to generalize more, leading to relaxed selection on close mimicry (Joron, 2003). The data presented here (Fig. 6) provide some support for this idea. Among the tiger subrings analyzed here, pattern mimicry appears to be very good *within* subrings; however, mimicry declines if we consider the larger tiger ring encompassing the three subrings. As more mimics participate in a ring, perhaps mimicry need not be so good: a broadly mimetic pattern may be sufficient to fool avian predators, who must generalize more to avoid making a costly mistake.

A final observation is that differences between the tiger rings appear to be due more to pattern contrast (amplitude) than to shape (contributions of marking size); perhaps avian predators make broad generalizations in terms of contrast but attend to specific cues related to marking size. Without further analysis, this observation remains purely speculative, but it is easy to see how objective pattern quantification of butterfly wing patterns can generate new and testable hypotheses about mimetic signals. It will be beneficial to consider pattern mimicry in light of the frequent new discoveries about the genetics (Joron et al., 2011; Heliconius Genome Consortium, 2012) and developmental processes (Joron et al., 2006) influencing mimicry by *Heliconius* and related genera.

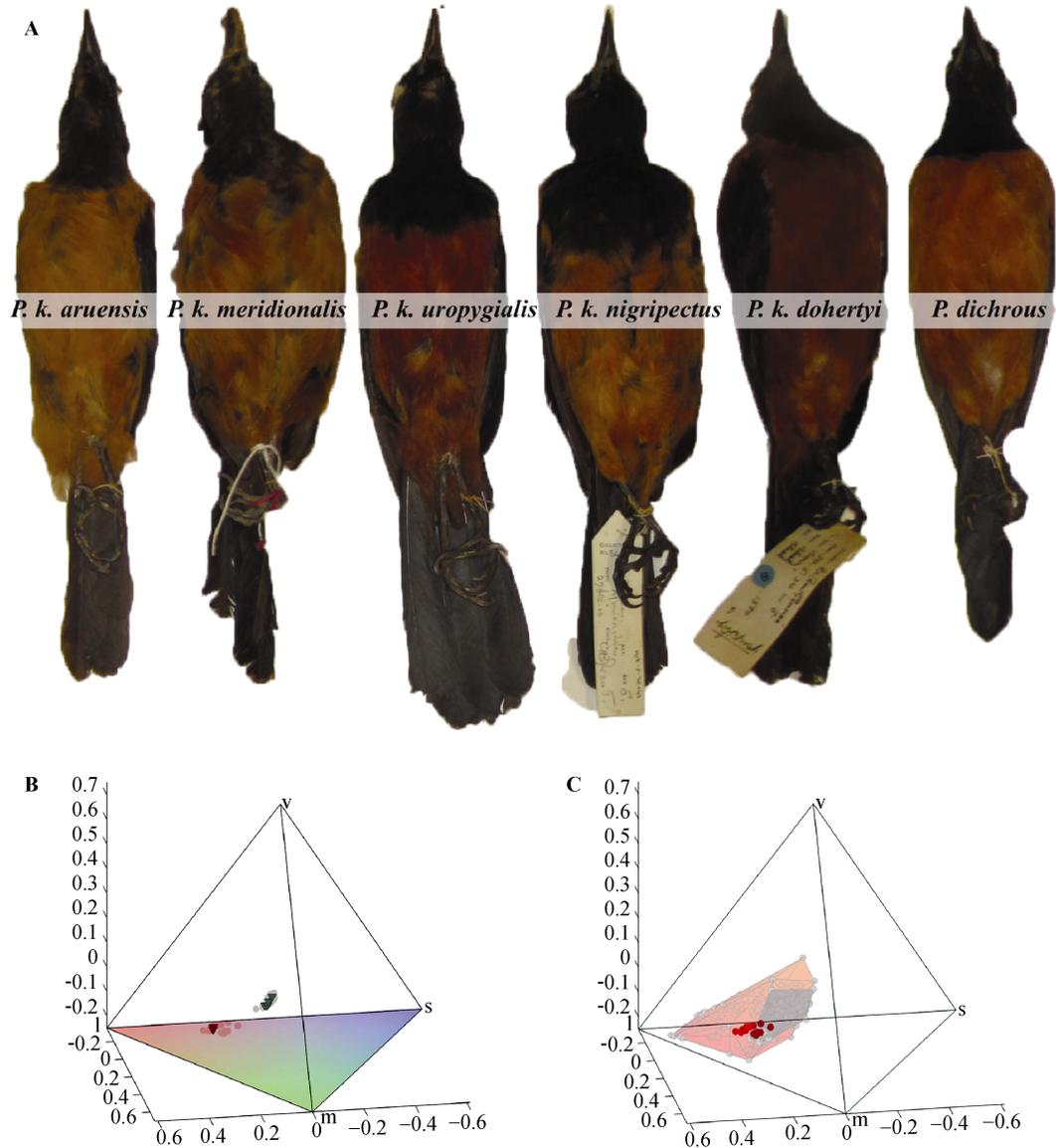
#### 4.4 Shared plumage patterns in toxic pitohuis

**Toxically defended Pitohuis are potential avian Müllerian mimics. Here I use models of avian color vision to test the hypothesis that one subspecies of the variable pitohui has convergently evolved plumage colors that match, to a bird's eye, those of the hooded pitohui. I also investigate whether the toxic red plumage of pitohuis is likely produced by carotenoid or**

#### **phaeomelanin pigments.**

Although Müllerian mimicry is common in the insect world, proposed examples of Müllerian mimicry in birds are extremely rare. Potential candidates for avian Müllerian mimics are bird species in the endemic New Guinea genus *Pitohui*, which are chemically defended by a toxic alkaloid (Dumbacher et al., 2000). Pitohuis and one species in a separate New Guinean genus *Ifrita* *kowaldi* are the only known birds with chemical defenses (Blount and McGraw, 2008). Their skin and feathers contain batrachotoxin, the same poison used by many *Phyllobates* frogs (Blount and McGraw, 2008), which is believed to provide defense against predators such as hawks, snakes, and even human hunters (Dumbacher and Fleischer, 2001). The two most toxic species are the hooded pitohui *Pitohui dichrous* and the variable pitohui *Pitohui kirhocephalus*, whose ranges overlap broadly. *P. dichrous* and six subspecies of *P. kirhocephalus* share a remarkably similar color pattern ('the mimetic phenotype'), which consists of a deep red belly and back that contrasts with a black head, wings, and tail (Fig. 7). Dumbacher and Fleischer (2001) used a molecular phylogeny and maximum likelihood estimates to determine whether the mimetic phenotype is an artifact of shared ancestry or the result of selection for Müllerian mimicry. They demonstrated that the mimetic phenotype is best explained by shared ancestry except in the case of *P. k. dohertyi*, a subspecies of *P. kirhocephalus*. *P. k. dohertyi* is nested deep within a clade that appears to have lost the mimetic phenotype (Fig. 8), which *P. k. dohertyi* appears to have re-evolved. This result is consistent with the idea that Müllerian mimicry may explain the strong visual resemblance between the *P. k. dohertyi* and *P. dichrous* phenotypes.

If *P. k. dohertyi* is a Müllerian mimic of *P. dichrous*, how successful is it in achieving plumage color mimicry? Table 2 indicates that the red back and black throat, breast and wing plumage patches of *P. k. dohertyi* are a very good match to corresponding patches of *P. dichrous*. For comparison, the color differences between the other 'mimetic phenotype' subspecies of *P. kirhocephalus* (similarity explained by shared ancestry) and *P. dichrous* are also shown in Table 2. If *P. k. dohertyi* is constrained in its ability to produce mimetic colors, we might expect it to be a poorer match to *P. dichrous* relative to the *P. kirhocephalus* subspecies for which shared ancestry explains plumage similarity. However, this does not appear to be the case. Although *P. k. meridionalis* achieves a very good color match to *P. dichrous* across almost all plumage patches, the other *P. kirhocephalus* subspecies are comparable to *P. k. do-*



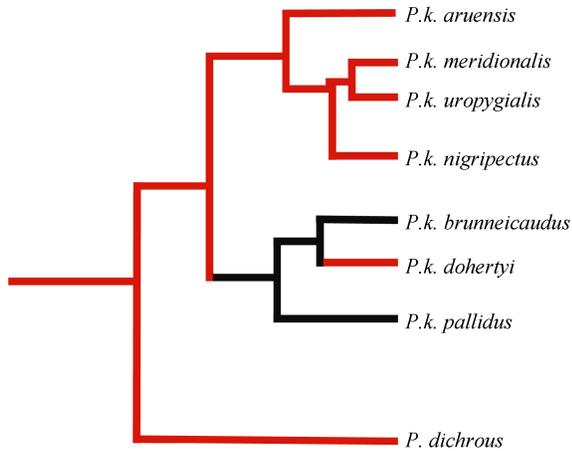
**Fig. 7** Müllerian mimicry in toxic Pitohuis

**A.** Five subspecies of the variable pitohui *Pitohui kirhocephalus* are shown alongside a hooded pitohui *Pitohui dichrous*. Although the remarkably similar color patterns between *P. kirhocephalus* and *P. dichrous* can be explained largely by shared ancestry, Müllerian mimicry may explain the strong visual resemblance between the *P. k. dohertyi* and *P. dichrous* phenotypes. Photos are copyright NHM and taken by M. C. Stoddard. **B.** From the perspective of a bird, the red and black coloration of *P. k. dohertyi* (depicted as triangles) is just as good a match to the red and black colors of *P. dichrous*, relative to other *P. kirhocephalus* subspecies. **C.** The red colors exhibited by chemically defended *P. kirhocephalus* and *P. dichrous* are shown relative to other carotenoid (orange polyhedron) and phaeomelanin (brown polyhedron) colors in more than 50 other avian species (Stoddard and Prum, 2011). Modeling was done using VS cone-type sensitivities.

**Table 2** Comparison of *Pitohui* plumage colours

	<i>P. k. aruensis</i>	<i>P. k. meridionalis</i>	<i>P. k. uropygialis</i>	<i>P. k. nigripectus</i>	<i>P. k. dohertyi</i>	
crown	<b>1.8</b>	<b>0.5</b>	<b>2</b>	<b>1.7</b>	4.1	
back	<b>1.9</b>	<b>2.2</b>	7	4.3	<b>0.8</b>	
rump	13.1	3.6	18.7	18	16.2	
throat	3.6	<b>1.1</b>	<b>1.9</b>	<b>0.9</b>	3.1	<i>P. dichrous</i>
breast	3.6	<b>1.4</b>	<b>2.3</b>	2	<b>2.2</b>	
belly	<b>2.3</b>	<b>1.3</b>	4.7	<b>1.6</b>	3.4	
wing	3.9	<b>0.8</b>	<b>1</b>	<b>1.8</b>	<b>1.1</b>	

Shown here are Just-Noticeable Differences between plumage color patches on subspecies of *P. kirhocephalus* and *P. dichrous*. Boxes with JND < 3 are shown in bold, indicating that colors are very similar. Visual modeling was done from the perspective of an average VS cone-type, using cone-type proportions for peafowl. See main text for details.



**Fig. 8** A simplified phylogeny showing the relationships of *Pitohui kirhocephalus* and *Pitohui dichrous*, adapted from Dumbacher and Fleischer (2001)

Relative branch lengths are not depicted. Branches with the mimetic red-black phenotype are shown in red and those with the non-mimetic phenotype are shown in black. One large clade of *P. kirhocephalus* lost the mimetic phenotype early in its evolution, but one race, *P. k. dohertyi*, has re-evolved the phenotype. Thus, *P. k. dohertyi*'s similarity to *P. dichrous* is consistent with the hypothesis that Müllerian mimicry may explain the visual resemblance of their plumage patterns.

*hertyi* in their degrees of color match. In fact, *P. k. dohertyi* achieves the best color mimicry of any *P. kirhocephalus* subspecies in terms of its match to the red back of *P. dichrous*. Modeling of *P. dichrous* and *P. kirhocephalus* colors in avian color space confirms the close match of *P. k. dohertyi* to *P. dichrous* (Fig. 7B). The black and red colors of *P. k. dohertyi* fall in the exact same regions of color space as *P. dichrous* and the other *P. kirhocephalus* subspecies.

If Müllerian mimicry is profitable for *P. k. dohertyi*, why hasn't mimicry evolved in the other *P. kirhocephalus* subspecies within the large clade that lost the mimetic phenotype? One possibility is that different suites of local predators impose different selective pressures on mimetic phenotypes. For instance, in a geographic region lacking visually oriented avian predators, selection for mimetic plumage might be relaxed. In this study, I modeled pitohui colors from the perspective of a potential VS predator, such as a raptor. However, it would be intriguing to model pitohui plumage colors from the perspective of snakes, which often use a combination of chemical and visual cues to locate their prey (Greene, 1997), to determine how effective pitohui mimicry might be in the eyes of diverse predators.

It is also interesting to consider whether there is any-

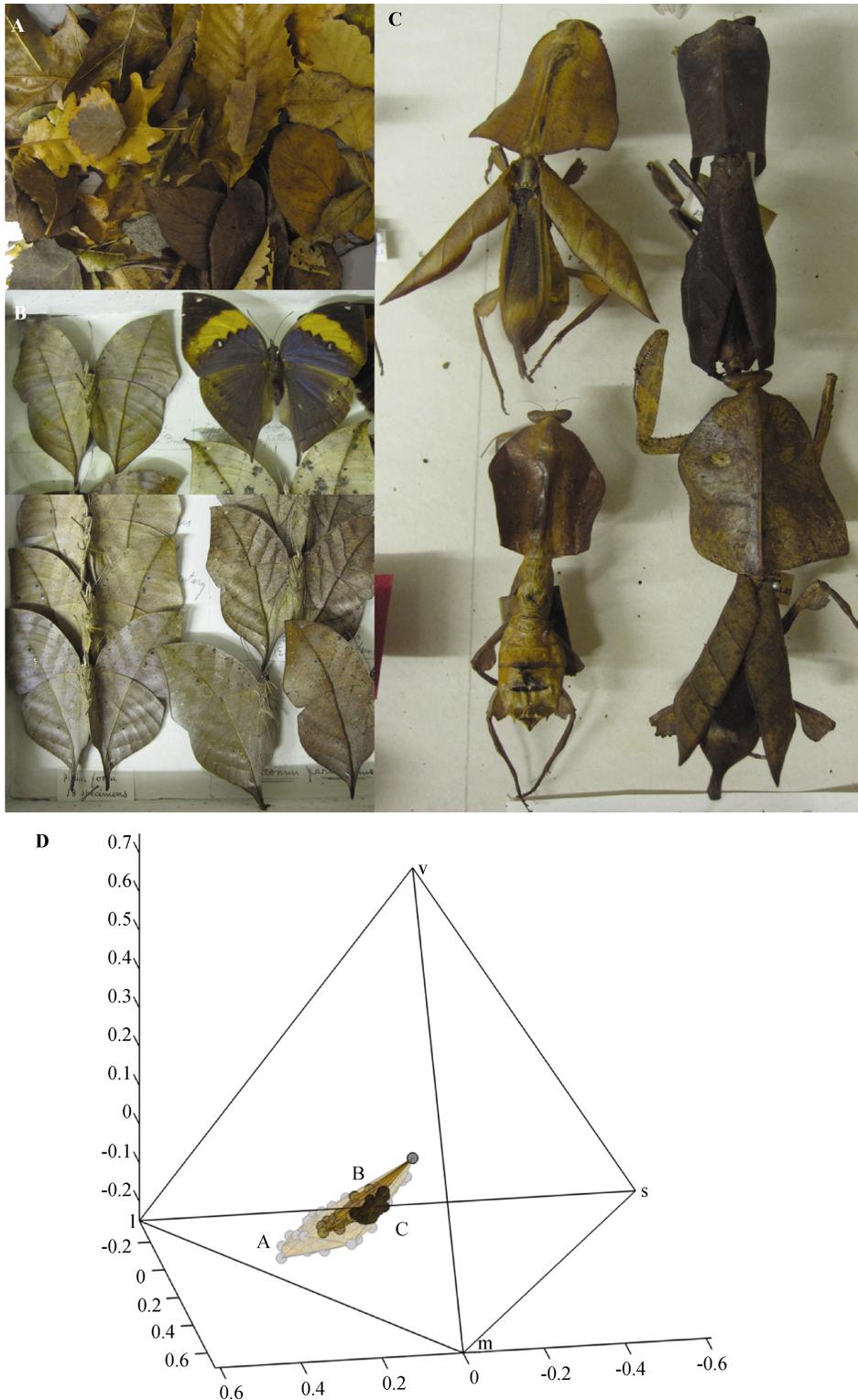
thing unique about the color signal exhibited by toxic pitohui plumages. It is unknown whether their toxic red-orange feather colors are derived from carotenoid or phaeomelanin pigments (Blount and McGraw, 2008). Comparison of pitohui red feather colors to a diverse set of carotenoid and phaeomelanin pigments (Fig. 7C) from more than 50 avian species (Stoddard and Prum, 2011) shows that pitohui feather colors fall well within the signaling gamut of other red, orange, and brown plumage colors in the avian world. Pitohui colors appear to fall squarely within the carotenoid distribution but at or just beyond the red-orange limit of the phaeomelanin distribution. If phaeomelanin is responsible for red pitohui colors, it produces them in a way that would extend the known range or gamut of phaeomelanin-based colors in Aves (Stoddard and Prum, 2011).

## Masquerade

### 4.5 Dead leaf-mimicking butterflies and mantids

*Many butterflies (Lepidoptera) and praying mantises (Mantodea) masquerade as dead leaves. Here I use an avian tetrahedral color space model to test the hypothesis that dead leaf-mimicking Kallima butterflies and Deroplatys mantids match the colors of dead leaves.*

Mimicking leaves has been classified as Batesian mimicry by some and crypsis by others but is now considered to be masquerade, which occurs when an organism is misidentified as an inedible or innocuous object (Skelhorn et al., 2010a; Stevens and Merilaita, 2009). Only recently has empirical work shown that organisms can benefit from masquerade (Skelhorn et al., 2010b) and that the strategy is most effective when masqueraders are rare relative to their models (Skelhorn et al., 2011). The empirical work to date has been on caterpillars masquerading as twigs, and it seems plausible that dead leaf-mimicking butterflies and praying mantises benefit in similar ways (Fig. 9). To a human observer, the dead leaf-mimicking insects are remarkable: Wallace (1867) called *Kallima* butterflies (Fig. 9B) "the most wonderful and undoubted case of protective mimicry in a butterfly," remarking that the butterflies' ventral sides are "some shade of ash or brown or ochre, such as are found among dead, dry, or decaying leaves" and that down the wings runs "a dark curved line exactly representing the midrib of a leaf, and from this radiate on each side a few oblique lines, which serve to indicate the lateral veins of a leaf." But the most "extraordinary part of the imitation," according to Wallace (1867), are the "representations of leaves in every stage of decay, variously blotched and mildewed and pierced with holes,



### Fig. 9 Masquerade in insects

Dead leaf-mimicking butterflies (*Kallima* spp.) (B) and dead leaf-mimicking mantids *Deroplatys truncata* (C) are striking mimics of dead leaves (A). D. From a bird's-eye view, the colors of dead leaf-mimicking butterflies and mantids fall well within the color range of natural dead leaves. Photos are copyright UMZC (B-C) and taken by M. C. Stoddard. Modeling was done using VS cone-type sensitivities.

and in many cases irregularly covered with powdery black dots gathered into patches and spots, so closely resembling the various kinds of minute fungi that grow on dead leaves that it is impossible to avoid thinking at

first sight that the butterflies themselves have been attacked by real fungi!" The mimicry achieved by many praying mantises, including the dead leaf mantis *Deroplatys truncata* and the giant dead leaf mantis *Deroplatys truncata*

*platys desiccata*, appears to be equally sophisticated.

I compared the dead leaf-mimicking colors of *Kallima* butterflies (Fig. 9B) and *Deroplatys* mantids (Fig. 9C) to the colors of an assemblage of dead leaves (Fig. 9A) collected from the Cambridge University Botanic Garden. Although the dead leaves were not specific to the tropical Asian habitats of *Kallima* and *Deroplatys* species, I tested the general hypothesis that *Kallima* and *Deroplatys* insects effectively mimic the colors of dead leaves. Fig. 9D shows that, from the perspective of a VS cone-type avian predator, the leaf-mimicking colors of *Kallima* and *Deroplatys* species fall within the color range of real dead leaves, indicating that the color mimicry is realistic to a bird's eye. A few important points can be made from this simple observation. First, it seems very unlikely that color is the only important aspect of leaf mimicry, since the organism's resemblance to leaf texture and even behavior (some dead leaf-mimics reportedly wobble in the wind to mimic the motion of a natural dead leaf) are probably equally crucial. It would be fascinating to use artificial prey experiments (e.g., Cuthill et al., 2005) to manipulate different properties (color, pattern, texture) of dead leaf-mimics to determine which cues may be most essential for effective mimicry. Second, empirical work so far (Skelhorn et al., 2010b) indicates that predator cognition (i.e., recognition and identification) may be more important than sensory capabilities in driving the evolution of masquerade. If this is true, then avian predators may become better in time at recognizing dead leaf-mimics vs. dead leaves, even if their colors remain indistinguishable. It would be interesting (albeit challenging) to determine how avian discrimination decisions are influenced both by the degree of color mimicry between dead leaf-mimics and their models (sensory processing) and by past experience (cognitive processing). If cognitive processes like learning and experience prove to be better predictors of predator discrimination, then we might expect selection by sensory systems for close color mimicry to be relaxed. Perhaps once dead leaf-mimics achieve a certain degree of color mimicry, there is no added benefit to improved color mimicry because cognitive processes become dominant. It would be productive to compare behavioral experiments with birds to the predictions of visual models to determine whether color categorization (grouping similar colors together) is at work. This approach has been used to demonstrate that foraging chicks generalize groups of colors, such that the results of behavioral tests often deviate from the predictions of discrimination models (Jones et al., 2001; Ham and Osorio, 2007).

Are dead leaf-mimics effective because they are dif-

ficult to detect (crypsis) or because they are easily misclassified (masquerade)? A limitation of visual models is that they cannot distinguish between these alternatives. The analysis here shows that the mimics' colors are indistinct from a backdrop of dead leaves (Fig. 9D), but it doesn't show whether this makes the mimetic insects challenging to detect, readily misidentified, or both. Thus, color vision models must be coupled with more advanced models of higher-level visual and cognitive processes, as well as with behavioral experiments, to better understand how dead leaf-mimics escape predation.

## 5 Conclusion

As dominant predators, birds are extremely important receivers of visual mimetic signals. However, the extent to which bird vision has shaped the evolution of mimetic signals is largely unknown. We are now in an excellent position to investigate defensive visual mimicry from the perspective of birds. We know more about the vision of birds (at least in terms of spectral sensitivity) than we do any other vertebrate group apart from primates, and the techniques available for quantifying color, luminance, and pattern from the avian visual perspective have flourished in recent years. In this paper, I developed five case studies to show how incorporating the avian visual perspective can dramatically improve our understanding of defensive mimicry and masquerade. I argue that this is not simply a matter of applying fancy new tools to obvious questions but rather a means to generating new and testable hypotheses based on rigorous and objective quantification. Although the sample sizes used in the case studies were low, and as such the results should be considered preliminary at best, my aim was to highlight the huge scope for investigating defensive mimicry from a bird's-eye view and to promote future empirical work in this overlooked area. Ultimately, incorporating the predator's sensory system into broad questions about mimicry will enhance our understanding of the selective pressures driving signal evolution.

Several recent studies of aggressive mimicry by brood parasites have successfully embraced models of avian vision, shedding new light on the evolution of egg mimicry and rejection (Avilés, 2008; Cassey et al., 2008; Vikan et al., 2009; Spottiswoode and Stevens, 2010; Stoddard and Stevens, 2010; Yang et al., 2010; Spottiswoode and Stevens, 2011; Stoddard and Stevens, 2011), chick mimicry (Langmore et al., 2011), and host exploitation (Tanaka and Ueda, 2005; Tanaka et al., 2011). For example, avian visual modeling of common cuckoo eggs demonstrated that the degree of egg pattern and color mimicry achieved by the cuckoo is precisely related to the discrimination abilities of its target host

(Fig. 10) (Stoddard and Stevens, 2010; 2011). The same may be true in Australia, where new evidence suggests that *Chalcites* bronze-cuckoos have evolved remarkable mimicry (to a bird's eye) of host chick skin coloration (Langmore et al., 2011). Even beyond the egg and chick stage, a parasitic nestling can exploit the perceptual system of its host: to mimic an extra host gape, Horsfield's hawk-cuckoo *Cuculus fugax* chicks have a special yellow wing-patch that could function as a super-normal visual stimulus, inducing parents to increase feeding (Tanaka et al., 2011). Thus, the integration of perceptual modeling into studies of mimicry has helped to revolutionize the study of brood parasite-host dynamics (Safran and Vitousek, 2008) and could have a similar impact on studies of predator-prey interactions and other forms of defensive mimicry.



**Fig. 10 Incorporating the avian visual perspective has helped shed new light on cuckoo-host evolution**

**A.** Common cuckoos *Cuculus canorus* exhibit aggressive mimicry when they sneak their eggs into the nests of other species. The cuckoo eggs (left-hand column) are often, but not always, an excellent match (to a bird's eye) to eggs laid by host birds (right-hand column). Photos are copyright NHM and taken by M. C. Stoddard. **B.** A common cuckoo chick begs for food from its foster parent, a reed warbler *Acrocephalus scirpaceus*. Photo credit: D. Kjaer.

An inherent challenge to studying mimicry is that it can be difficult to determine when something is actually mimetic; often species resemble each other due to shared phylogeny, adaptation to a similar environment, or similar mode of perceptual exploitation (Schaefer and Ruxton, 2009). To properly quantify mimicry, it is essential to design focused, controlled studies with relevant comparisons. For example, it is interesting but insufficient to say that the colors of the common cuckoo resemble those of the sparrowhawk. To prove that this is mimicry, it should be shown that Cuckoo feather colors are more similar to sparrowhawk colors than they are to the plumages of birds from diverse and unrelated taxa.

Exploring the relationship between avian vision and

mimetic signals has broader implications for understanding the evolution of aposematism. In evaluating Batesian and Müllerian mimicry, my focus in this paper was on how well the mimic matched the model rather than on the wider (and more challenging) question of what makes an effective warning pattern. It remains unclear why aposematic colors are often bright, colorful, and conspicuous, and several explanations have been proposed (Sherratt and Beatty, 2003; Ruxton et al., 2004; Stevens and Ruxton, 2012). One possibility is that these colors are simply easier for predators to recognize, while an alternative explanation is that bright coloration helps models appear distinct from undefended mimics. A vast body of work in avian predators shows that birds often show unlearned and learned avoidance of certain colors and patterns such as red, yellow, black, and stripes (reviewed in Endler and Mappes, 2004; Ruxton et al., 2004), and several recent experiments have revealed which specific color and pattern cues may matter most to avian predators (Niskanen and Mappes, 2005; Aronsson and Gamberale-Stille, 2008). Integrating findings about the form and function of aposematism into research on defensive visual mimicry will help to clarify the highly complex relationships between mimics, models, and the viewers to which they signal.

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