

# *Are tropical butterflies more colorful?*

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## Are tropical butterflies more colorful?

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**Abstract** There is a common and long-standing belief that tropical butterflies are more striking in their coloration than those of cooler climates. It has been suggested that this is due to more intense biotic selection or mate selection in the tropics. We tested whether there were differences in coloration by examining the dorsal surface color properties of male butterflies from three regions of the western hemisphere: the Jatun-Satcha Reserve in lowland Ecuador (tropical), the state of Florida, USA (subtropical) and the state of Maine, USA (cool temperate). We digitally photographed the dorsal wing and body surface of male butterfly specimens from Maine, Florida, and Ecuador. For each photograph, we analyzed the mean and variation for the color-parameters that are thought to be related to colorfulness; namely Hue, saturation and intensity. Overall, the Ecuadorian sample exhibited more varied intensity, saturation, and Hue compared to the other regions. These results suggest a more complex assemblage of colors and patterns regionally and on a butterfly-by-butterfly basis in the tropics. The greater complexity of colors within each butterfly in our Ecuadorian sample suggests that tropical butterflies are indeed more 'colorful', at least by some measures. Possible reasons for this include stronger predation pressure selecting for aposematism, greater species diversity selecting for camouflage or warning coloration against potential predators, and easier recognition of potential mates in a species rich environment.

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### Introduction

It is a common belief that insect colors and coloration patterns are more striking in the tropics and subtropics compared to higher latitudes. This belief, now rarely discussed in the literature, appears to date back to the first European naturalists who visited the tropics (e.g. Wallace 1878, 1879) and studied adaptive coloration in detail (Wallace 1878, 1879; Poulton 1890). It has been accepted as one of the ecological differences between the temperate and tropical zones (MacArthur 1969), and it also persists in contemporary natural history accounts (e.g. Lambertini 2000). However, museum curators, who see the full range of species in tropical insect faunas, are more skeptical of this idea (J. Weintraub per. comm.); noting that there are large numbers of bland-colored species in addition to the most colorful ones.

Discussion of bright coloration in insects usually focuses on aposematism (Wallace 1879; Poulton 1890). Evolution of bright coloration might be explained through a Fisherian runaway process (Fisher 1930), which favors stronger signals and co-evolved prey defense mechanisms (i.e. toxicity). Another possibility is that biased generalization (or peak-shift) of predators can favor brighter prey (Gamberale and Tullberg 1996). The result is predators that avoid the most exaggerated signals as the prey become brighter and more striking. However, there are certain fitness costs associated with conspicuous visual signals due to the resource requirements associated with making bright colors and displaying structures (Blount et al. 2012), which may balance the advantage of being brighter.

Explanations for the supposedly greater colorfulness of low latitude insects focus on the idea that there is more intense predation and more intense co-evolution in warm aseasonal climates (Wallace 1879; Poulton 1890; MacArthur 1969). In these cases, the major selective influences are

thought to be: (1) stronger selection for striking aposematic coloration due to more intense year-round predation pressure, and (2) the need for more easily recognizable coloration patterns for use in finding mates due to the richness of tropical insect communities (Wallace 1879).

If one is to properly understand how communities function, and how the high and low latitudes differ ecologically (MacArthur 1969), it is important to establish whether there is evidence for latitudinal gradients in insect coloration. The concept of 'colorfulness' is elusive and subjective; but one can define various objective aspects of color that might be expected to contribute to what most observers would define as colorfulness. These include: (1) color intensity, the 'strength' or 'brightness' of a color, (2) color saturation, the purity of a color, and (3) Hue, the relative relationship to the primary colors. Whether other animals whose sensory perceptions differ from ours (Théry and Gomez 2010) would find similar colors and combinations striking is unknown. However, there are many indications that there is a common perception of colorfulness and striking patterning among humans and other species. For instance, eyespots on Lepidoptera that are perceived by humans as colorful and striking, also seem to effect predator behavior (Ruxton 2005; Stevens et al. 2007). Additionally, poisonous animals from many different taxa (e.g. snakes, beetles, butterflies, wasps, mollusks) that are noted by humans for their coloration are also strongly avoided by their (non-human) predators (Ruxton et al. 2004; Ruxton 2005; Saporito et al. 2007).

Here we chose a well-studied group known for its striking coloration: the butterflies (distinguished from moths by diurnality, club-shaped antennae and absence of frenulum). Butterflies are an ideal group to study because they are large insects of widespread interest, and are well documented in many parts of the world. We compared the butterfly faunas along a latitudinal series that included temperate and subtropical regions of North America as well as the tropical rainforest of South America. Our hypothesis was that tropical species are more colorful and complex in coloration compared to the temperate regions.

## Methods

### Locations

In this study, we compared the butterfly faunas of three localities in the Western Hemisphere. To represent cooler climates and the subtropics, we included two well-studied butterfly faunas from Maine and Florida. The North American species were compiled from state lists of Opler and Warren (2003) and Opler et al. (2004), their replacement (USGS 2013), and Pelham (2008). These lists were modified on the basis of additional advice of Lepidopterists (J. Weintraub per. comm.) at the Philadelphia Academy of Sciences; synonyms and strays were removed from the lists. Florida extends 24°–30° North (mean annual temperature 19–24 °C), and includes warm

temperate and subtropical climates. Maine ranges from 43° to 47° North and has cold temperate and boreal climates (mean annual temperature 4–8 °C) (Muller 1982).

To represent a tropical butterfly fauna, we chose a list developed in a study of one large (approximately 2,000 hectares) lowland tropical nature reserve (Murray 1996) in Ecuador because no contemporary list of butterfly species encompasses the whole of any nation in the tropics. This reserve is much smaller than either of the US states, but its butterfly fauna is much richer. The reserve is described as 'a patchwork of habitats'; its central core is 70 % forest, and its edges are a mosaic of primary forest, secondary forest, including scrub and pasture land (Murray 1996). As such, it represents a similar range of habitats compared to Maine or Florida. Murray (1996) used a combination of sampling methods including hand held nets, bated traps, and the rearing of field-collected larvae, from a 10 km radius, over a period of 3 years. This exceptional thoroughness makes it likely that the butterfly species list obtained by Murray includes most of the species present in the area (J. Weintraub per. comm.). We used Murray's species list of 811 species on the assumption that the habitat mosaic of the reserve will be representative of the broader tropical region of Amazonia, and provide a comparable range of habitats to those found in Maine and Florida.

### Choice of specimens

For all three regions, we photographed museum specimens selected from the aforementioned species lists. Following the advice of lepidopterists, the best-preserved male specimens of each species were selected and photographed. From Maine and Florida, 50 and 89 species, respectively, were available from the complete list (Appendix S1 and S2). Tropical species (Ecuador,  $n = 108$ ) were randomly selected (Appendix S3) using a pseudo-random number generator from the species list in the appendix of Murray (1996).

From all three regions the HesperIIDae were excluded because it is a relatively large family in which members are generally drab in color. This allowed our study to concentrate on the other families of butterflies, which evidently rely heavily on coloration for aposematism and/or mate identification (and thus are most likely to show geographical differences in coloration resulting from differences in natural selection, if these are indeed important). Complete lists of the species that were included in this study are presented in Appendix S1, S2 and S3.

### Photographic procedure

We photographed 50, 89, and 108 species of butterflies from Maine, Florida, and Ecuador, respectively. These were from specimens in the Lepidoptera collections of American Museum of Natural History, New York, and the Academy of Natural Sciences, Philadelphia.

Photographs were taken of the dorsal wing/body surface in a standard light box containing 5100 k halogen bulbs with a Sony DSC-F828 digital camera at a resolution of 8 megapixels. A standardized background was used during photography so that it could be easily removed during post processing. Furthermore, all pictures were taken in RAW format with a Kodak color card so minor variations in lighting that might effect color detection could be corrected. Following the photographic procedure, lighting and coloration were standardized in Adobe Photoshop CS2 and the background was removed. After post-processing, the images were saved as TIFF images for use in photo-analysis.

### Butterfly color data collection

We analyzed the HSI (Hue, saturation, intensity) color-space because these three variables are generally associated with what is termed 'colorfulness' (Hill and McGraw 2006). Hue is defined as the wavelength within the visible spectrum at which energy output is the greatest (Hue involves stronger similarity of reflected light to a primary color). Saturation is defined as the expression of the relative bandwidth within the light spectrum (high saturation involves a relatively 'pure' color, with a narrow range of wavelengths reflected from the surface), and intensity is defined as the brightness of the color (the proportion of incident light reflected). HSI color space may not reflect how all-potential predators see the butterflies. However, there are many predators of butterflies ranging from invertebrates to mammals (Turner 1979; Brower et al. 1985; Pinheiro 1996); and, resolving an animal's perspective is difficult (as well as computationally burdensome). Therefore, we used the HSI color space, which corresponds to the tristimulus color recognition mechanism of human perception (Hill and McGraw 2006). This allowed us to test the common-belief predicted by a human's point of view.

A photo-analysis program was written in MATLAB for the specific purpose of analyzing our butterfly photos in a standard manner. The program resized the images to 300 × 300 resolution and analyzed the color properties of all pixels in the photo, not including the background area, which was given zero values for HSI variables during post processing. Antennae were excluded from the analysis as many museum specimens

had lost these structures. A sample specimen from our study is shown in Supplementary Fig. 1.

The MATLAB program measured all variables on a scale ranging from zero to one. Hue, which is a circular scale, was broken at the interface between red and blue; it was linearized where red was at the higher end of the scale and blue was at the lower end of the scale. After our program analyzed all pixels, the final outputs were "whole butterfly" statistics; the mean and standard deviation were given for each color variable. These were used in statistical analysis because they would indicate the average color, purity of color, and brightness for each species. Additionally, the standard deviations of these variables indicate the complexity of coloration in the butterflies' dorsal surfaces.

### Statistical analysis

The variables included in the analysis of dorsal surface coloration included the means and standard deviations of Hue, saturation, and intensity. These variables were measured on a scale ranging from zero to one by our photo-analysis program; therefore, no further transformation was required. Species color-measures were organized by their region (ME, FL, EC) and analyzed using discriminant function analysis (DFA). The multivariate model was developed using forward selection (F-to-enter = 2.5) and a Monte Carlo Test with 499 permutations. Wilks' lambda ( $\lambda$ ) was used to derive the multivariate F-statistic and *p* value, respectively. The individual variables were interpreted using their approximate F-statistic, structure coefficient, and tolerance values. Furthermore, groups were classified using the "between-group" F-matrix and a jackknifed classification technique. Finally, individual butterfly scores were plotted along the first two canonical axes and 95 % confidence intervals were constructed from regional means.

## Results

The basic statistics for the mean and standard deviation of dorsal wing/body surface Hue, saturation, and intensity are reported in Table 1. These variables did not exhibit any significant correlations (Pearson's Coefficient > 0.60); therefore, all variables were included in DFA (Table 2).

**Table 1** Basic statistics for each of the measured variables in the analysis of dorsal butterfly wing surfaces

	Basic statistics (n = 247)					
	Mean Hue	Hue SD	Mean saturation	Saturation SD	Mean intensity	Intensity SD
Min	0.00	0.00	0.05	0.03	0.10	0.06
Max	0.93	0.94	0.95	0.32	0.90	0.37
Mean	0.13	0.17	0.52	0.19	0.48	0.18
Median	0.09	0.07	0.52	0.18	0.44	0.17
SD	0.16	0.22	0.17	0.05	0.21	0.06
Interquartile Range	0.05	0.24	0.24	0.07	0.40	0.09

**Table 2** Pearson's correlation matrix showing the interrelationships among variables

Pearson's correlation matrix (n = 247)						
	Mean Hue	Hue SD	Mean saturation	Saturation SD	Mean intensity	Intensity SD
Mean Hue	1					
Hue SD	0.43	1				
Mean saturation	-0.28	-0.44	1			
Saturation SD	-0.10	0.21	0.42	1		
Mean intensity	-0.06	-0.41	0.01	-0.27	1	
Intensity SD	-0.07	0.32	0.10	0.56	-0.30	1

**Table 3** Variable means by region

	Regional means for all variables		
	Maine	Florida	Ecuador
Mean Hue	0.13	0.11	0.15
Hue SD	0.08	0.08	0.29
Mean saturation	0.57	0.49	0.51
Saturation SD	0.17	0.17	0.21
Mean intensity	0.49	0.6	0.37
Intensity SD	0.15	0.15	0.22

Comparison of regional data means

*Hue*

The mean Hue did not vary significantly among regions. Florida and Ecuador had roughly the same average value; Maine had a slightly lower value. The variation in color (Hue SD) within each sample of butterfly specimens was greatest in Ecuador, being about 3 times greater than either of the other two regions.

*Saturation*

Purity of the Hue (mean saturation) was greatest in Maine but the differences among regions were not large. However, variation of color purity (saturation SD) was greatest in the Ecuador. Florida and Maine had the same amount of variation in color saturation.

*Intensity*

Color intensity was greatest in the Floridian sample (mean intensity) and varied most (intensity SD) in the Ecuadorian sample. A complete set of results for each variable by region is presented in Table 3.

Multivariate comparison of regional coloration and classification

Discriminant function analysis (DFA) successfully separated the three regions based on the aforementioned color variables (n = 247,  $\lambda = 0.52$ ,  $F = 19.34$ ,  $p < 0.001$ ). The forward selection process identified 5

variables with F-to-enter of 2.5 or greater. The only variable that did not enter the model after 5 iterations and 499 permutations was Mean Hue. The first variable to load was intensity SD followed by, mean intensity, Hue SD, mean saturation, and saturation SD, respectively. All of the variables except mean Hue had highly significant individual F-ratios and increased the performance of the final model (Table 4).

Two classification functions were derived during the model development. The first function was the principal in the classification process (eigenvalue = 0.78) and accounted for 90 % of the total data dispersion (inset correlation of 0.66). Intensity variation (intensity SD) was the first variable to load in this function (structure coeff. = 0.59) followed by Hue SD (structure coeff. = 0.52), suggesting that individual and regional color variation is controlling the statistical model. Classification function 2 accounted for the remaining 10 % of the variation in the butterfly color data (eigenvalue = 0.09) and had an inset correlation of 0.29. The first variable to load in this function was Mean Saturation (structure coeff. = -0.95) followed by saturation SD (structure coeff. = 0.71) and Mean Intensity (structure coeff. = 0.61). Among all variables in both canonical functions, the intensity variables exhibited the highest levels of independence (tolerances = 0.76 and 0.90 for Intensity SD and mean intensity, respectively). Discriminant statistics are presented in Tables 4 and 5.

Mean canonical scores for Maine, Florida, and Ecuador were -0.46, -0.92, and 1.00 for canonical function 1, respectively. For function 2, canonical scores for the aforementioned regions were -0.53, 0.26, and 0.07. Individual species scores were plotted along the first two principal axes and 95 % confidence intervals were applied allowing for visualization of regional data groups (Fig. 1). Groups separated readily using this technique; Ecuador separated visually from the other two groups, which overlapped each other to a greater extent than either one overlapped the Ecuadorian sample (Fig. 1). These visual results mirror that of the multivariate model and classification matrixes. The between-group F-matrix shows a large difference between Ecuador and Florida ( $F = 35.78$ ) as well as Ecuador and Maine ( $F = 18.18$ ). Finally, the classification matrix shows a high degree of overall accuracy (62 %), with the highest rate of regional accuracy occurring for the Ecuadorian samples. Maine and Florida samples were

more often confused with each other than the Ecuador samples suggesting a distinct separation in coloration for the tropical species (Table 5).

color characteristics compared to those of North America. Our analysis suggests that the sample of species from the Ecuadorian fauna contain more individual and overall variability in coloration than samples from Florida and Maine. The principal differences in coloration between temperate and tropical butterflies were found to be in the amount of variation for intensity and Hue. Thus, Ecuadorian butterflies as a set were more variable in color and brightness compared to Maine and

## Discussion

Overall, we found that the tropical butterflies of our Ecuador sample were significantly different in certain

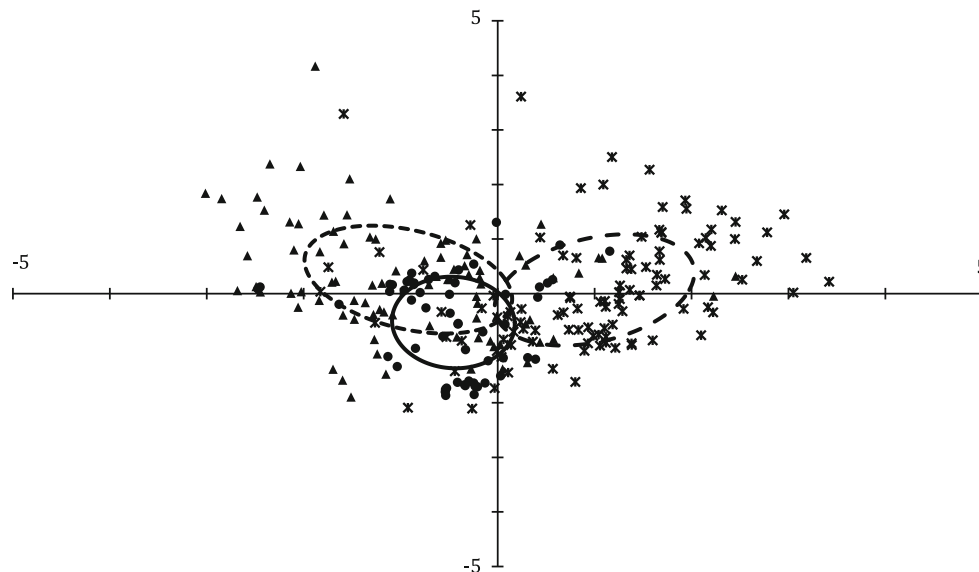
**Table 4** Discriminant function statistics in the comparison and classification of latitudinal regions and butterfly species, respectively

Discriminant function analysis					
Final model statistics					
n	df	$\lambda$	F	p-value	
247	490	0.52	19.34	< 0.001	
Stepping summary					
Variable	Order entering model	F (+ enter, -remove)	$\lambda$	Individual F-ratio	p value
Intensity SD	1	47.86	0.72	47.86	< 0.001
Mean intensity	2	26.45	0.60	36.71	< 0.001
Hue SD	3	10.57	0.55	28.84	< 0.001
Mean Saturation	4	5.29	0.53	23.31	< 0.001
Saturation SD	5	2.82	0.52	19.34	< 0.001
Mean Hue	Did not enter	N/A	N/A	N/A	N/A
Variable statistics					
Variable	Structure coeff. 1	Structure coeff. 2	Tolerance		
Intensity SD	0.59	0.01	0.76		
Mean intensity	-0.45	0.61	0.90		
Hue SD	0.52	0.01	0.61		
Mean saturation	0.26	-0.95	0.52		
Saturation SD	-0.01	0.71	0.54		
Mean Hue	N/A	N/A	N/A		

$\lambda$  Refers to Wilks' Lambda, which is used to calculate the F-statistics. F to enter/remove refers to the difference in model fit with the inclusion or removal of the respective variable: Larger values indicate greater importance during model development. N/A indicates that those statistics are not applicable because that variable did not increase the fit of the model

**Table 5** Discriminant function classification statistics and jackknifed classification matrix

Classification and related statistics				
Classification statistics				
	Canonical function 1	Canonical function 2		
Eigenvalue	0.78	0.09		
Canonical correlation	0.66	0.29		
Portion of dispersion	0.9	0.10		
Maine mean score	-0.46	-0.53		
Florida mean score	-0.92	0.26		
Ecuador mean score	1.00	0.07		
Jackknifed classification matrix				
	Maine	Florida	Ecuador	% Correct
Maine	26	19	5	51
Florida	25	54	10	61
Ecuador	26	7	75	69
Cumulative	80	82	92	62



**Fig. 1** Discriminant function plot with individuals shown as points, which are associated with the following group indicators: (1) Asterisks—Ecuador, (2) Triangles—Florida, and (3) Cir-

cles—Maine. The long-dashed, solid, and short-dashed lines represent 95 % confidence intervals for the groups Ecuador, Maine, and Florida, respectively

Florida. Furthermore, the tropical butterflies assessed in this study were also more variable in color saturation (purity). This interesting regional difference in the amount of variation in all three color properties suggest a more complex assemblage of colors on a butterfly-by-butterfly basis in the tropics; potentially a result of patterns involving more visual contrasts across the wing.

This result is consistent with the hypothesis that tropical butterflies have more ‘striking’ coloration. Patterns of internal contrast on wings (often black patterns with red, orange or yellow colors) are commonly found in aposematic species and function to enhance the effectiveness of aposematic signalling (Aronsson and Gamberale-Stille 2009, 2012). The greater within-butterfly contrast found in our tropical sample is consistent with the effect of stronger predator selection for visibility or through sexual selection. Alternatively, there might be some other selective effect that would produce more variability amongst tropical butterflies. One possibility is that in a very diverse butterfly fauna such as Ecuador, there is stronger selection for distinctive coloration/patterning to facilitate mate identification.

Among the factors that may ultimately cause increased selection for more striking coloration are the low light levels under the dense evergreen tropical forest canopy (Hill and McGraw 2006), which reduce the effective signalling of aposematic coloration. Thus, contrasting color patterns would outperform consistent coloration in this light condition and should be favored. This enhanced visual display in darker forest environments has been identified in bird plumage color patches (Marchetti 1993), and, by analogy, may also apply to butterflies. Also, low subcanopy light levels may select for patterns that can readily be discriminated/selected by potential mates in a more diverse butterfly community.

However, it is necessary to bear in mind that much of the Ecuadorian Jatun Satcha reserve is non-forested (Murray 1996) and subject to much higher light levels. Another possibility is that the greater overall species richness of the tropics increases the selective pressure for distinctive color mosaics that are used in mate recognition or are a result of sexual selection. Finally, there is no indication from these results that the well-documented formation of mimicry rings amongst tropical South American butterflies (Benson 1972) has suppressed the range of coloration relative to the temperate zone.

Despite these interesting findings, we must acknowledge that the latitudinal pattern detected in this study may be a result of a greater number of distinct evolutionary lineages of tropical butterflies. The Ecuadorian fauna contains butterfly subfamilies (e.g. Heliconiinae) that are absent or poorly represented in Maine and Florida, whereas families present in those two states are all present in the Ecuador sample.

#### Uncertainties and recommendations for further studies

There is a need for caution in making evolutionary and ecological conclusions, since we could not quantify the ambient light condition of the butterflies’ natural habitat and differences in predator vision. Although many predation simulation experiments have revealed the importance of aposematic signals (Ruxton et al. 2004), it would be informative to test the role of color Hue, saturation, and intensity separately on predators’ avoidance behavior. It is also necessary to bear in mind that bird and insect vision includes the near-UV (Lyytinen et al. 2001; Théry and Gomez 2010. Olofsson et al.



2010), which was not included in this analysis. It is possible that if we had included characteristics of the near UV range in our analyses, we would have obtained different results. Another limitation of this study is that it only included a set of faunas from the Western Hemisphere, and did not include other tropical regions (e.g. central Africa, SE Asia) or other temperate regions (e.g. Europe, north-eastern Asia, or temperate Australia).

Nevertheless, this work represents a necessary first step in the study of the biogeography of color patterns in insects, and how coloration varies at regional or habitat scales. We hope that this example may lead to other studies using a broadly similar approach to coloration patterns which will reveal how the structure of communities, and the selective forces that shape them, vary on the broad scale.

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