

Ecological Study of Lizard Dewlap Colour and Area

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Summary: This paper reports on the statistical analysis of data collected by Benjamin Bartholomew and his team to (i) investigate the relationship between Anoles' dewlap colour and their environment and (ii) the relationship between abundance levels of Anoles and their dewlap sizes. Primary analysis indicates that for *Anolis cybotes*, an increase in elevation increases hue and saturation, but decreases brightness while an increase in precipitation increases saturation. For *Anolis semilineatus*, an increase in elevation and precipitation increase brightness. We also find that for *Anolis semilineatus*, lizards in densely populated areas have smaller dewlaps.

1 Introduction

Male *Anolis* lizards possess dewlaps - extensible throat fans. An *anole* will extend the dewlap to attract females to mate with. These dewlaps vary in colour and visual signals on dewlaps are more easily detected by receivers when signals stand out from the environment. Dewlap signal variation can be explained by abiotic and biotic factors. In this paper, we perform statistical analysis to evaluate how abiotic factors affect the colour and how abundance affects dewlap size.

The two research questions are:

- (i) How does the environment affect an *Anoles*' dewlap colour.
- (ii) How does the population density affect an *Anoles*' dewlap size (area).

The first hypothesis stems from the theory that animals adapt to best survive in their environment. By analyzing how colours change according to climate and location, we can evaluate how this theory works for *Anoles*.

The second hypothesis is from the intuition that lizards that live closer together don't require dewlaps to be as big as those living further from each other. The former implies a high population density while the latter implies a low density.



Figure 1a: A lizard from *Anolis carolinensis* flashes his dewlap to attract females. (Photo: Ken Slade)

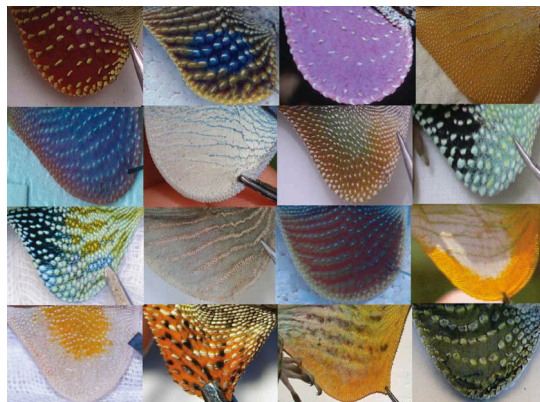


Figure 1b: The photographs show how dewlaps differ by species ¹. (Photo: David Hillis and Richard Glor)

¹ Species in order from right to left and top to bottom: *A. pulchellus*, *A. sericeus*, *A. liogaster*, *A. longitibialis*, *A. cobanensis*, *A. gorgonae*, *A. cristatellus*, *A. chlorocyanus*, *A. reconditus*, *A. christophei*, *A. cuprinus*, *A. new species*, *A. lineatopus*, *A. annectens*, *A. baleatus*, *A. auratus*

A summary of the data and changes made in preparation for analysis are given in Section 2. A description of the statistical methods used and results are given in Section 3. The conclusion follows with additional discussion in Section 4.

2 Summary of Data

The dataset contains information about the sex, species, population abundance level ², dewlap area, snout-vent length and the colour of the dewlap. Colour is made up of hue, saturation and brightness values ³.

In addition to physical data on lizards, we have data on the environment where the specimen was collected such as precipitation ⁴, temperature ⁵, tree cover ⁶ and elevation ⁷.

The data was collected on various sites on the island of Hispaniola by Ben and his fellow researchers over the summers of 2016 and 2017. Both research questions are answered using the same dataset. The data was provided in two copies; (I) has three additional samples.

- I. dataset with environmental variables, colour data (Hue, Saturation, Brightness)
- II. dataset with environmental variables, abundance, area and SVL data.

The data is filtered for only male adult lizards of *cybotes* and *semilineatus* because good quality data wasn't available for the other species.

² Output from mark recapture model developed by Luke Frishkoff.

³ Output from ImageJ software in conjunction with ColourHistogram plugin.

⁴ Data scraped from <http://chelsa-climate.org/>

⁵ Data scraped from <http://chelsa-climate.org/>

⁶ Data scraped from <https://landcover.usgs.gov/glc/TreeCoverDescriptionAndDownload.s.php>

⁷ Data scraped from <http://www.worldclim.org/>

| | Miniumum | Median | Mean | Maximum | Standard Devation | NAs |
|--------------------------------------|----------|--------|-------|---------|-------------------|-----|
| Hue | 0.065 | 0.120 | 0.118 | 0.143 | 0.014 | 0 |
| Saturation | 0.066 | 0.178 | 0.235 | 0.672 | 0.134 | 0 |
| Brightness | 0.607 | 0.789 | 0.784 | 0.889 | 0.043 | 0 |
| Temperature (°C) | 16.00 | 23.90 | 23.01 | 26.90 | 3.681 | 10 |
| Precipitation (mm/year) | 892 | 1303 | 1491 | 2433 | 448.6 | 10 |
| Elevation (m) | 2.0 | 390.0 | 583.7 | 1878.0 | 619.9 | 10 |
| Tree Cover (% Cover) | 0.00 | 69.00 | 60.67 | 100.00 | 36.38 | 10 |
| Abundance* (Samples/m ²) | 0.09 | 3.66 | 9.12 | 40.42 | 13.13 | 81 |
| Area (mm ²) | 41.1 | 205.3 | 269.6 | 743.7 | 176.1 | 0 |
| Snout-Vent Length (mm) | 30.0 | 50.4 | 49.5 | 72.1 | 12.2 | 8 |

Table 1: Summary of Covariates (Filtered for male *cybotes*, *semilineatus*)

2.1 Additional information:

- Data is well balanced in terms of species: 99 (56%) *cybotes* and 85 (44%) *semilineatus*.
- Precipitation, temperature, tree cover and elevation are missing for 10 samples. This is due to the lack of GPS coordinates for these observations, which are required for the data generation.
- There are 81 missing values for abundance in the the second dataset. This is because some of the locations where lizards were collected are not in scope of the mark recapture model.

- After filtering for missing values, for the colour data (I) we have 90 *cybotes* and 84 *semilineatus* and 40 *cybotes* and 60 *semilineatus* for abundance data (II).

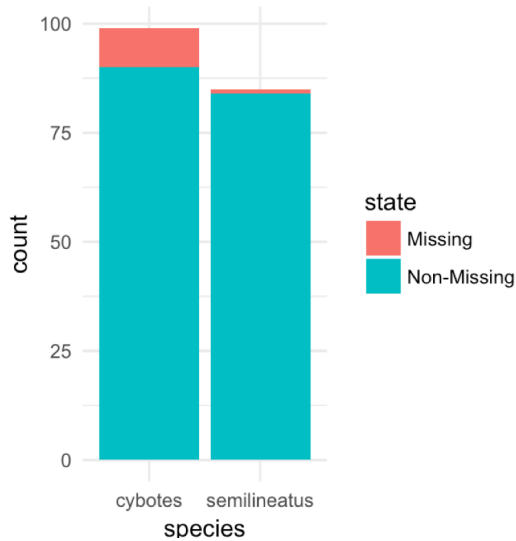


Figure 2a: Missing values for (I)

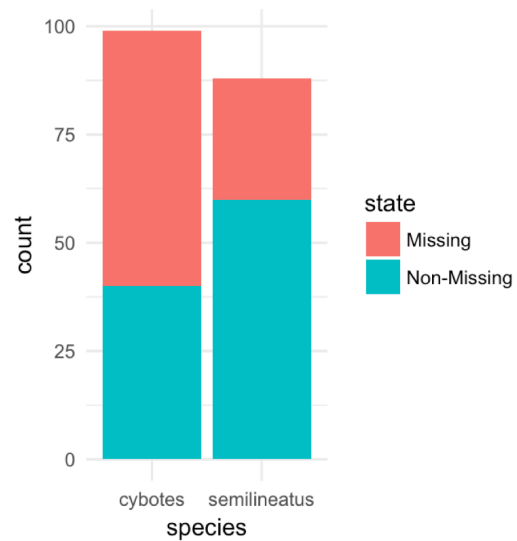


Figure 2b: Missing values for (II)

- We will fit our abundance model leaving out the missing values since the data is missing in a systematic way by location.
- Missing values are often clustered by collection site. Although some sites contain both missing/non-missing values, we can see that *Matadero*, *Las Coles*, *Los Haitises* and other locations do not contain any data on abundance.



Figure 3: Map of observations of missing/non-missing values of abundance

- To put Hue, Saturation and Brightness on the same scale, we need to centre and standardize them by their respective means and standard deviations.

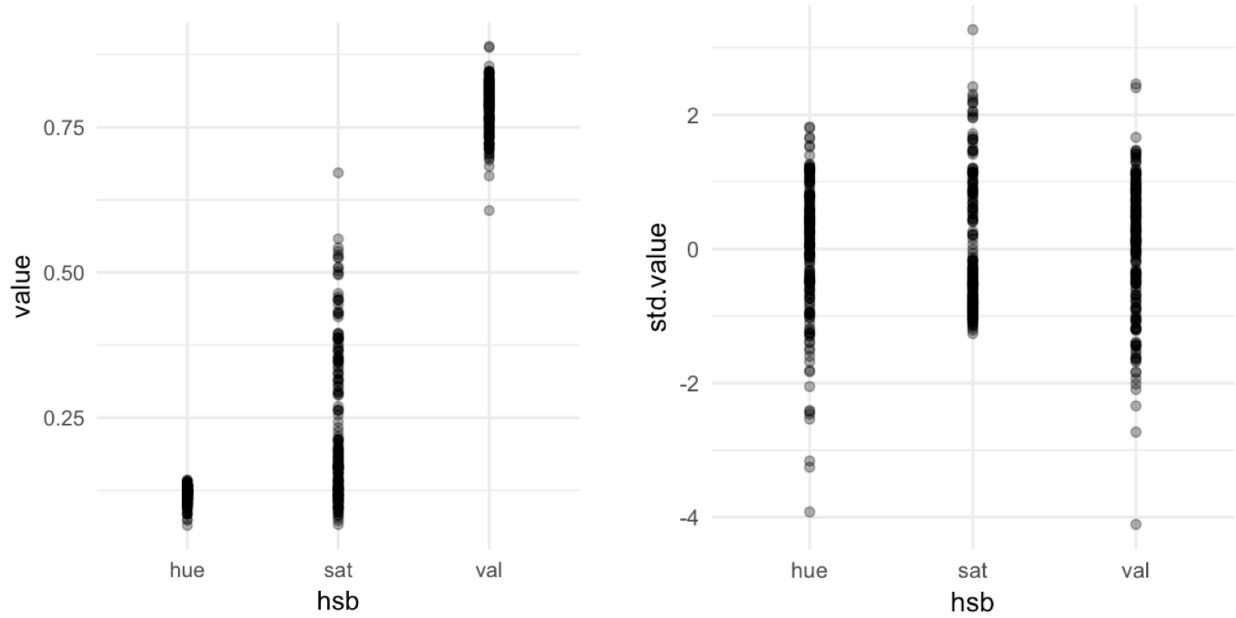


Figure 4a: Raw HSB Values Figure
(Before Transformation)

4b: Standardized HSB Values
(After Transformation)

| | Miniumum | Median | Mean | Maximum | Standard Devation |
|------------------------------|----------|--------|-------|---------|-------------------|
| Hue | 0.065 | 0.120 | 0.118 | 0.143 | 0.014 |
| Saturation | 0.066 | 0.178 | 0.235 | 0.672 | 0.134 |
| Brightness | 0.607 | 0.789 | 0.784 | 0.889 | 0.043 |
| Hue (Standardized) | -3.922 | 0.174 | 0.000 | 1.821 | 1.000 |
| Saturation (Standardized) | -1.261 | -0.421 | 0.000 | 3.270 | 1.000 |
| Brightness (Standardized) | -4.107 | 0.129 | 0.000 | 2.459 | 1.000 |

Table 2: Summary of raw and standardized hue, saturation, brightness

3 Statistical Methods & Results

3.1 Methods for Colour Question

To recap, our first main research question asks if environmental factors affect the colour of *Anolis* lizard's dewlaps. We fit a linear multivariate mixed model with colour as the response.

- Colour is broken down into hue, saturation and brightness using ImageJ software. We use a multivariate model to account for the correlations amongst them.
- Mahler (unique id) is included as a random effect because of the “long” format of the data with an indicator variable to identify which of HSB is being modelled.
- We include mahler nested in general locality as a random effect because we expect data from lizards collected in the same locality to be correlated.
- Elevation, precipitation, tree cover, species are included as fixed effects. We remove temperature from the fixed effects due to multicollinearity in our model which would lead to erroneous estimates. This is because temperature and elevation have a 99.4% correlation. We keep elevation in our model based on the collaborator's feedback on which variable is of more interest.
- Interactions between species and the environmental variables were statistically significant, thus the effect of the environment on colour depends on species.

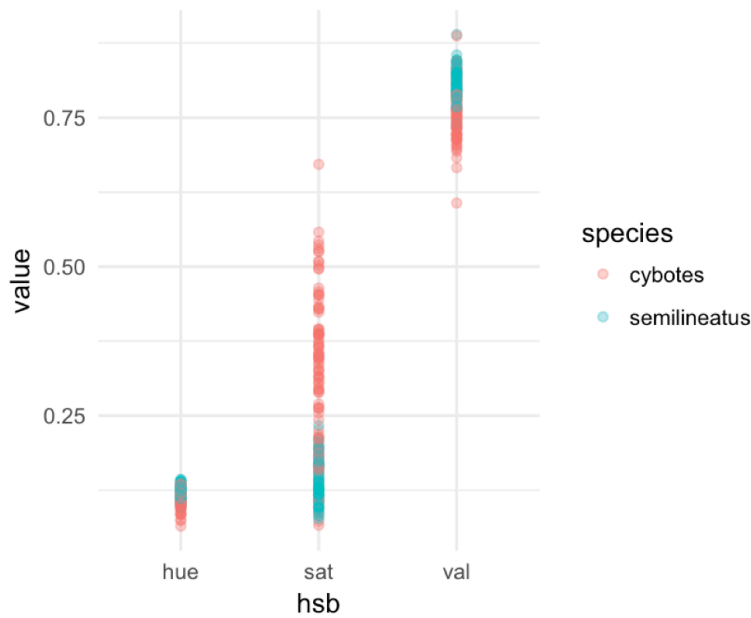


Figure 5: Raw Hue, Saturation and Brightness values by species.

We can see how HSB values are clustered by species. The exploratory plot is good motivation for checking for interactions between environmental effects and species.

3.2 Results for Colour Question

For *Anolis cybotes*, there is strong evidence that hue changes by +9.28E-06, saturation by +1.20E-04, and brightness by -1.91E-05 for each additional meter of elevation. There's strong evidence that saturation changes by +1.34 E-04 for each additional millimetre of precipitation.

For *Anolis semilineatus*, there is strong evidence that brightness changes by +2.07E-05 and weak evidence that hue changes by +3.5E-06 for each additional meter of elevation. There's moderate evidence that brightness increases by 2.15E-05 for each additional millimetre of precipitation.

Estimates and their corresponding *p*-values are produced below for each of HSB.

For Hue

| Effects of environment: | Estimate <i>cybotes</i> | <i>P</i> -Values <i>cybotes</i> | Estimate <i>semilineatus</i> | <i>P</i> -Values <i>semilineatus</i> |
|-------------------------|----------------------------|------------------------------------|---------------------------------|---|
| Elevation | 9.28E-06 | < 0.000*** | 3.50E-06 | 0.090 . |
| Precipitation | -8.54E-07 | 0.742 | -1.49E-06 | 0.614 |
| Tree Cover | -8.49E-05 | 0.012 | -3.46E-05 | 0.405 |

Statistical Significance Codes: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

For Saturation

| Effects of environment on | Estimate <i>cybotes</i> | <i>P</i> -Values <i>cybotes</i> | Estimate <i>semilineatus</i> | <i>P</i> -Values <i>semilineatus</i> |
|---------------------------|----------------------------|------------------------------------|---------------------------------|---|
| Elevation | 1.20E-04 | < 0.000*** | 1.99E-05 | 0.192 |
| Precipitation | 1.34E-04 | < 0.000*** | 1.46E-05 | 0.504 |
| Tree Cover | 1.56E-04 | 0.527 | -1.60E-04 | 0.602 |

Statistical Significance Codes: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

For Brightness

| Effects of environment on | Estimate <i>cybotes</i> | <i>P</i> -Values <i>cybotes</i> | Estimate <i>semilineatus</i> | <i>P</i> -Values <i>semilineatus</i> |
|---------------------------|----------------------------|------------------------------------|---------------------------------|---|
| Elevation | -1.91E-05 | 0.002** | 2.07E-05 | < 0.000*** |
| Precipitation | 9.04E-06 | 0.218 | 2.15E-05 | 0.011* |
| Tree Cover | 1.42E-04 | 0.134 | -1.01E-04 | 0.388 |

Statistical Significance Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

By evaluating our estimates by species, we can verify that the effect on colour differ by species.

- Visualizing how the fitted values change for each species by each environmental effect make the potentially significant interactions visible.
- The remaining two variables are held at their average values; ie. if we plot our fitted values by elevation, we hold the precipitation and tree cover at their respective means.
- Running a likelihood ratio test, we find that the interactions between species and the environmental variables are statistically significant (P -value < 0.0001). Thus, there is strong evidence that the environment's effect on colour depends on what species the lizard belongs to.

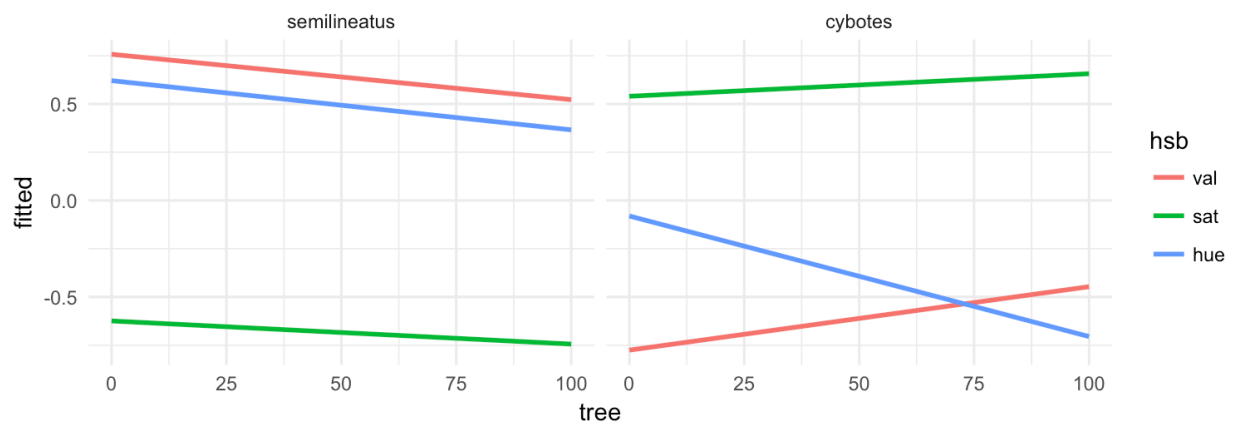


Figure 6a: Fitted HSB Values (Standardized) by Tree Cover

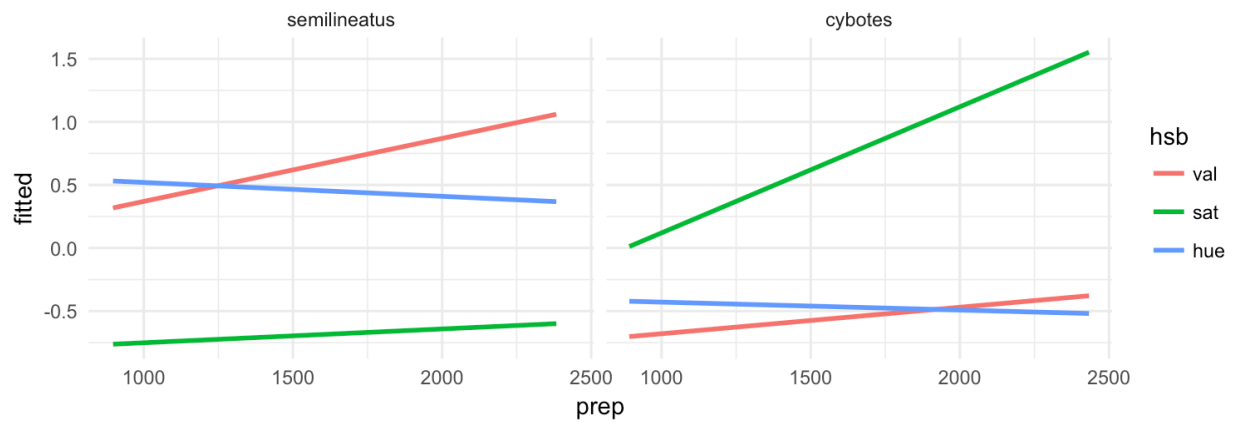


Figure 6b: Fitted HSB Values (Standardized) by Precipitation

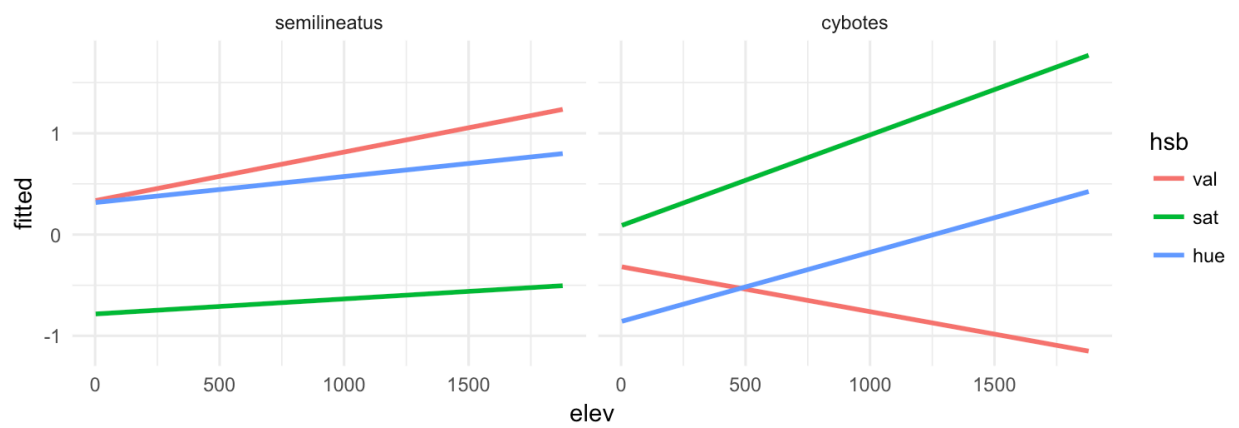


Figure 6c: Fitted HSB Values (Standardized) by Elevation

3.3 Model for Abundance Question

Our second research question asks if abundance levels of lizards affect the dewlap area of *Anolis* lizards. To answer this question we will fit a log-linear mixed model with response as the area.

- We include general locality as a random effect as we expect data from lizards collected in the same locality to be correlated.
- We include abundance as a fixed effect with the following covariates:
- SVL is included to control for the lizard's size as bigger lizards have bigger dewlaps.
- Elevation, precipitation and tree cover are included to control for the environment's effects on dewlap area. We are interested in abundance level's effect only.
- Upon testing, we find that there are interactions between species and abundance and species and SVL; these interactions are included in the model. (P -value < 0.01 for both)
- Plot of log-area vs abundance shows that the relationship may depend on species. Plot of fitted values vs abundance shows similar results.

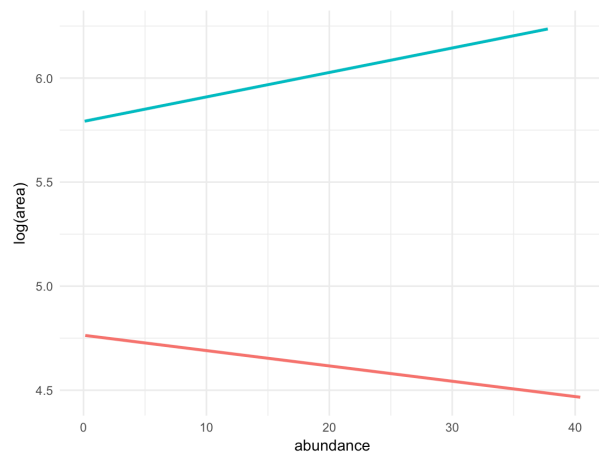


Figure 7a: Log area by abundance for both species

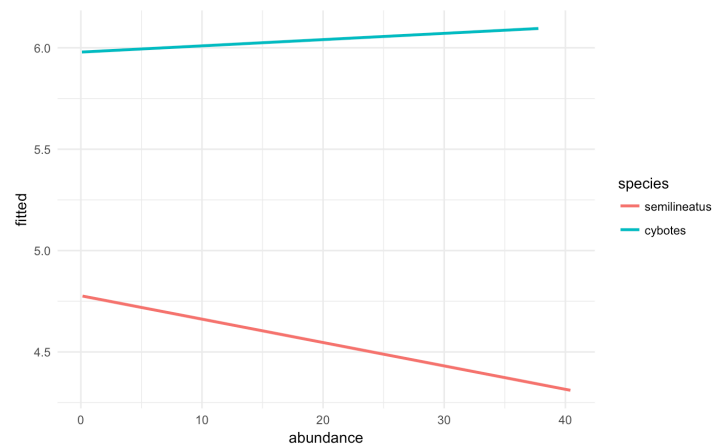


Figure 7b: fitted values by abundance for both species

3.4 Results for Abundance Question

There is strong evidence that for *Anolis semilineatus*, each unit increase in abundance level leads to a 1.28% decrease ⁸ in the area of the lizards' dewlap controlling for the lizard's size and the environmental factors.

| | Estimate <i>cybotes</i> | P-Values <i>cybotes</i> | Estimate <i>semilineatus</i> | P-Values <i>semilineatus</i> |
|------------------------------------|------------------------------------|------------------------------------|---|---|
| Effect of Abundance on Dewlap Area | 0.316% | 0.379 | -1.30% | 0.009** |

Statistical Significance Codes: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

3.5 Additional findings for Abundance

There is moderate evidence that for *Anolis cybotes* and *Anolis semilineatus*, an additional meter in elevation leads to a 0.025% and 0.026% decrease ⁹ in dewlap area respectively.

| | Estimate <i>cybotes</i> | P-Values <i>cybotes</i> | Estimate <i>semilineatus</i> | P-Values <i>semilineatus</i> |
|------------------------------------|------------------------------------|------------------------------------|---|---|
| Effect of Elevation on Dewlap Area | -0.025% | 0.0168* | -0.026% | 0.0339* |

Statistical Significance Codes: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

⁸ As the response is log-transformed the raw model estimate of -0.0129 should be multiplied by change in abundance, exponentiated and subtracted from 1 to get percentage decrease. ie. if you wanted to predict the percentage change in dewlap area for an increase of 10 in abundance you'd compute the following to calculate a 12% decrease: $1 - e^{(10 \times -0.0129)} = 12.1\%$

⁹ As response is log transformed we need to use a similar formula to calculate percentage change in area. The estimates are -0.000259 and -0.0002491 for *semilineatus* and *cybotes* respectively for the formula: $1 - e^{(\text{change in elevation} \times \text{estimate})} = \%$ decrease in dewlap area.

4 Conclusion & Discussion

The analysis of 174 lizards from various sites in Hispaniola indicate that for *Anolis cybotes*, an increase in elevation increases hue and saturation, but decreases brightness while an increase in precipitation increases saturation. For *Anolis semilineatus*, we find that an increase in elevation and precipitation lead to higher values of brightness.

Additional analysis found *Anolis semilineatus* lizards in densely populated areas have smaller dewlaps than those in sparsely population areas.

Secondary analysis indicates that *Anolis cybotes* and *Anolis semilineatus* have smaller dewlaps when they inhabit higher elevations.

The greatest limitation of our analysis is that our sample only includes *Anolis cybotes* and *Anolis semilineatus*. We also found that there are statistically significant interactions between species and the environmental effects as well as abundance, so our findings are very specific to each species. In order to have findings generalizable to *Anoles*, redoing the analysis with sufficient samples for various other species is desirable.

Tough we don't fully know the details of the data collection process, some bias is expected in the data especially for the abundance dataset where 87 of the 187 values were missing. An emphasis on getting well-balanced data for various species with sufficient samples would help us better generalize the findings.

If we had enough data for various species, we could use a mixed model with random slopes to capture how environmental variables affect colour differently for each species. Similarly, we could use random slopes to model how each abundance affects dewlap size for each species. If we found that a sufficiently high proportion of the species shared the same effect, we could conclude that for *Anoles* the effect exists. Magnitude of the effect would be computed by averaging the effects.

In addition to including data from more species, having more data for each species would grant more power, possibly increasing evidence for the effects. The findings from the secondary analysis should also be considered exploratory as the effect of environmental variables on dewlap size was not part of the research question.