**Effects of sex, age, habitat, season, and head size on feather color and brightness in great tits *Parus major***

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## Introduction

Variation in feather coloration is essential for communication tasks such as species recognition, predator deterrence, and attracting mates (Savalli 1995). Feather coloration can be broken down into chromatic and achromatic characters, which refers to color and brightness respectively. One cause of color variation is variation in the level of carotenoid pigments, which produce yellow and red coloration of the plumage of birds, and which can only be obtained through the diet (Fox 1976). There are many consequences of this variation in carotenoid pigments in birds such as deciding on a mate (Hill 1990) predator avoidance (Slagsvold & Lifjeld 1985). Furthermore, variation in plumage brightness has been shown to be a predictor of both reproductive success (Stein & Uy 2006) and habitat quality (Reudink et al. 2009).

The yellow coloration of great tit (*Parus major*) breast feathers is due to carotenoid pigments obtained through the diet (Partali et al. 1987), and it varies among individuals (Slagsvold & Lifjeld 1985). Therefore, variation of coloration in great tits is environmentally determined (Slagsvold & Lifjeld 1985). One factor that likely affects coloration is habitat, because deciduous habitats are a preferred habitat for great tits over coniferous habitats because of the more abundant resources (Mänd et al. 2005). In addition, bill morphology often affects diet (Grant & Grant 2006) and in great tits specifically, it has been observed that bill morphology changes by season because of the differences in available resources (Gosler 1987), which would then affect the amount of carotenoids an individual consumes. Therefore I will also look at how season and head and bill measurements may be related to feather coloration.

The data collected for this study are unique in that the sample size is very large and the data were collected over the span of several years. I have data from many repeatedly captured individuals, allowing me see changes of feather coloration from season to season and year to year. This allows for the testing of repeatability within an individual over time which is important for knowing if individuals change from year to year. I used reflectance analysis in order to get objective colorimetric measurements instead of human-subjective measures of animal coloration (Iskasson et al. 2008), as now widely utilized for this type of coloration analysis (Hill et al. 2006)

## Methods

### Feather Collection

From June of 2016 to June of 2019, Great Tits were captured at 14 sites of varying habitat quality, with some being coniferous habitats and some being deciduous habitats in County Cork and County Kerry, Ireland. The birds were captured via mist netting during the winter and at the nest box during the breeding season and each bird was given a leg ring with a unique ring number. Various data points were recorded for each captured individual before releasing them including the site of capture, whether the habitat type of the site of capture was coniferous or deciduous, whether the individual was caught during breeding season or during the winter, the age and sex of the individual, and measurements of the individuals bill length, bill depth, combined head and bill length, and skull width. Five yellow breast feathers from each side of the upper chest were also collected and were placed in individual envelopes with the bird's unique ring number recorded on the outside of the envelope.

Reflectance Measurements

To measure the reflectance spectrum, at least five feathers from each envelope were stacked on top of each other in order to get a more accurate reading of the pigment of the feathers (Quesada & Senar 2006). Then, I used a Mikropack DH-2000-BAL spectrophotometer with a nanometer range of 300-700nm in order to get the reflectance spectrum that encapsulates the full range of avian vision (Quesada & Senar 2006). I corrected the reflectance measurements for dark and light using a black standard and white standard. I measured the reflectance spectrum of the feathers from each sample against a non-reflective black background, specifically placing the probe on the yellow portion of the feather. I recorded three reflectance measurements for each sample, removing the probe and repositioning it in between each measurement, in order to help rule out stray readings. Measurements were redone if the reflectance spectrum graph was completely different than the typically observed spectrum graphs (**Fig. 1**). The final sample size was 1271 samples of feathers.

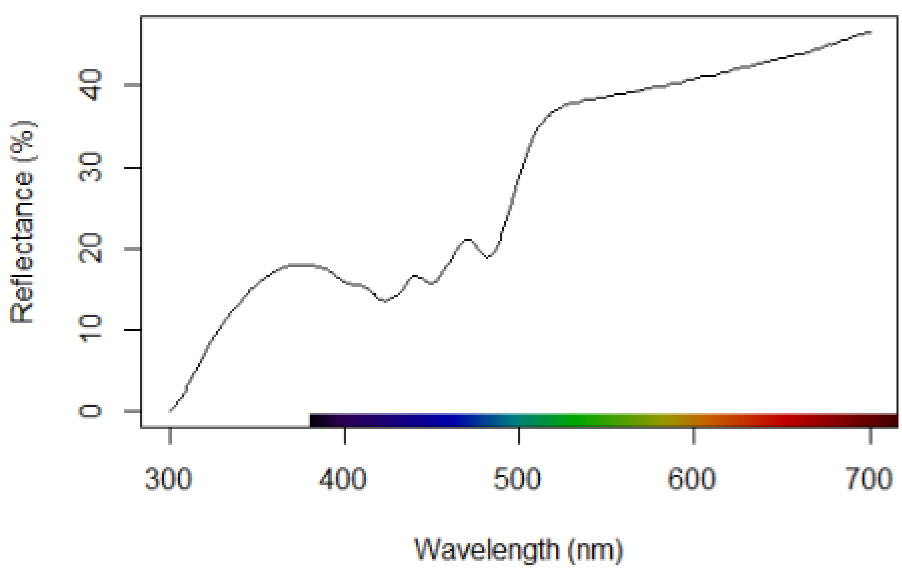



**Figure 1** Measured reflectance at each wavelength from range 300-700nm for a great tit yellow breast feather.

Visual Modeling

All the data modeling was done in R 4.1.2 software. My analysis was based on the visual modeling framework of Delhey et al. (2015) which models the coloration and brightness of the feathers as they would appear to a conspecific observer, taking into account multiple factors, such as the properties of the eye and its photoreceptors, as well as the properties of the environment, such as ambient lighting.

Each file contained a reflectance value for every 1 nm interval between 300-700 nm. First, for each sample, I adjusted for negative reflectance measurements (due to electrical noise) by increasing the minimum value to be equal to zero, and then increasing each reflectance measurement by the absolute value of that minimum value. Then, for each sample, I took the average reflectance spectrum of the three reflectance measurements. This average reflectance spectrum was then used for modeling.

I used the Pavo package vismod() function (Maia et al. 2019) to estimate the quantum catches in each of the four cones of a bird eye (ultraviolet, short, medium, long) for each sample. I used the assumptions of the photoreceptor characteristics of a blue tit, the brightness detection of a blue tit double cone, standard daylight illumination (D65), ocular transmission of a blue tit, and with the von Kries color correction.

I then measured the perceptual distances between each sample using the coldist() function, so that I could estimate how differently a feather would appear from another feather based on the visual model we used. The results of this model gave me values of Just Noticeable Differences (JND), a value that estimates whether an individual would be likely to perceive a difference between two different visual stimuli. The JND values differed depending on which analysis I did. When comparing categorical variables such as sex or age, I averaged all of the spectra in each category of the variable and then calculate the JNDs between those categories. The JND for each individual does not involve the averaging of spectra, and in this case, the JND is calculated using the differences between each individual and all other individuals. I assumed neural noise, relative photo receptor densities of 1, 1.92, 2.68, 2.70 (Hart et al. 2000), and a Weber fraction of 0.05. 95% confidence intervals for each JND were estimated using 1000 bootstraps with the bootcoldist() function.

I then converted the output of the color distances model for each individual into Cartesian coordinates. Using these x-y-z coordinates, I ran a principal component analysis to extract a single variable that explains the most variance of these coordinates (**Table 1**). I used the first principal component variable (PC1) for my analysis. A visual representation of color PC1 is shown in **Figure 2**.

| | PC1 | PC2 | PC3 |
|---|---|---|---|
| X | 0.8967506 | 0.4243217 | 0.12565606 |
| Y | -0.0748987 | -0.1343219 | 0.98810314 |
| Z | -0.4361520 | 0.8954936 | 0.08867208 |

**Table 1** Loadings of the principal components on each coordinate. The value of a principal component variable (PC) ranges from -1 to 1. The closer the value is to the absolute value of 1, the more that value contributes to the PC. The table shows that the x-axis contributes the most variance to PC1, the z-axis contributes the most variance to PC2, and the y-axis contributes the most variance to PC3.

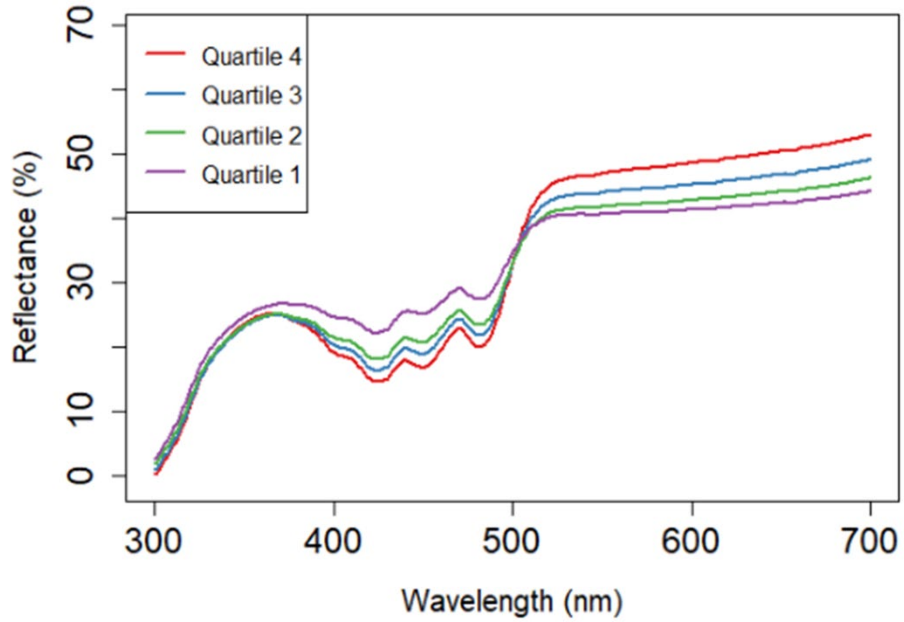



**Figure 2** Average spectrum for each quartile of PC1. Low PC1 corresponds to high reflectance at low wavelengths and low reflectance at high wavelengths.

<u>Data Analysis</u>

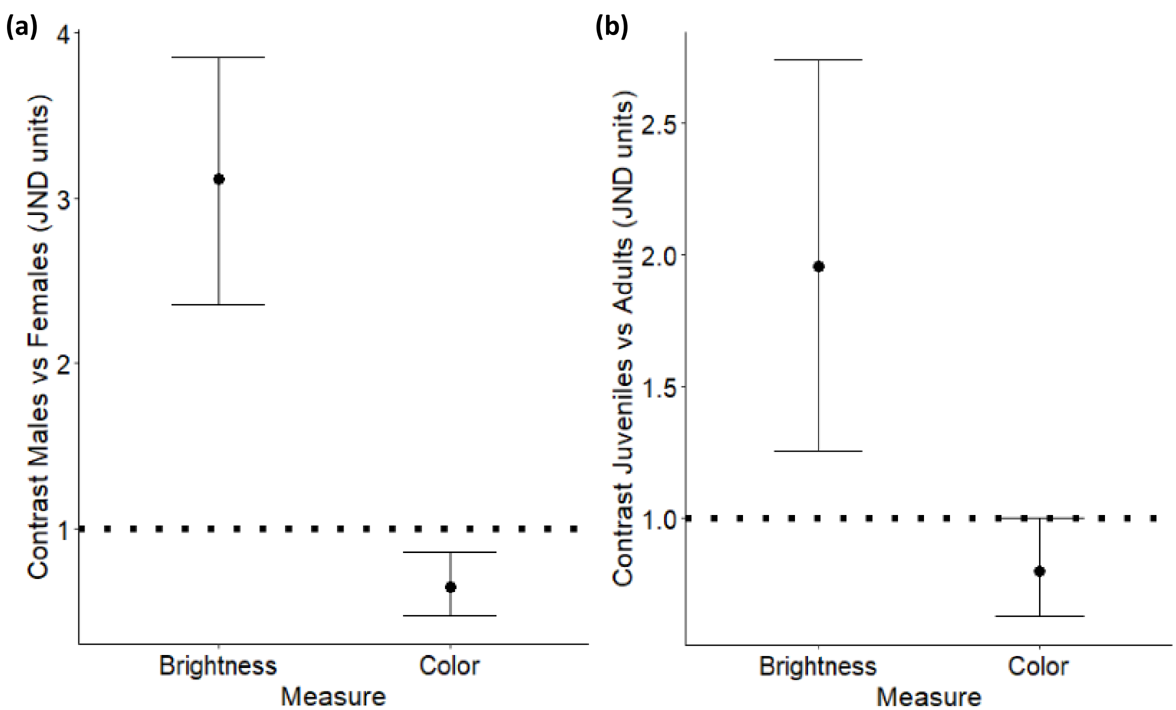
I tested whether there were differences in feather color and brightness between the sexes, age categories (juveniles or adults), seasons (winter or breeding season), and habitat type (coniferous or deciduous) by testing whether JNDs for these comparisons were greater than one. If the JND was greater than one and the 95% confidence interval did not cross over one, then this was considered evidence that a great tit receiver could perceive a difference in coloration or brightness between the feathers of the compared groups.

I also created a color and brightness model using lmer(), with color PC1 or brightness as the dependent variable and sex (male or female), age (adult of juvenile), wing length, tarsus length, season (winter or breeding season), bill depth, bill length, head and bill length, skull width, and habitat quality (coniferous or deciduous) as the independent variables, with individual identity added as a random effect, in order to check for the relationships between any of these variables and feather coloration, while accounting for other effects.

In addition, I used lmer() to see if feather color or brightness was related to past reproductive success, where color PC1 or brightness was the dependent variable and sex, age, and past clutch size or past number of chicks fledged were the independent variables, with individual identity added as a random effect and data only pulled from individuals who had a previous reproductive success measure and then a subsequent feather sample. I used glmer() to model if future reproductive success variables such as future clutch size or future number of fledglings, could be predicted by feather color or brightness, where future clutch size or future number of fledglings was the dependent variable, future referring to the clutch size or number of fledglings the year after the feathers used for the reflectance measurements were collected, and color PC1 or brightness, sex, and age were the independent variables, with individual identity added as a random effect and data only pulled from individuals who had a previous reproductive success measure and then a subsequent feather sample. Finally, I estimated the repeatability of feather color and brightness using the rpt() function in the rptR package, where the color PC1 or brightness was the dependent variable with the random effect of individual identity.

## Results

There were significant just noticeable differences (JND) in feather brightness between males and females (**Fig. 3a**) with males having brighter feathers, and between juveniles and adults (**Fig. 3b**) with adults being brighter, but no significant JND of feather color for either comparison. There were also significant JNDs in feather brightness and feather color between winter and breeding season (**Fig. 3c**) with feathers being brighter during breeding season. There were no significant JNDs in feather brightness or feather color based on the habitat of the individual (**Fig. 3d**).



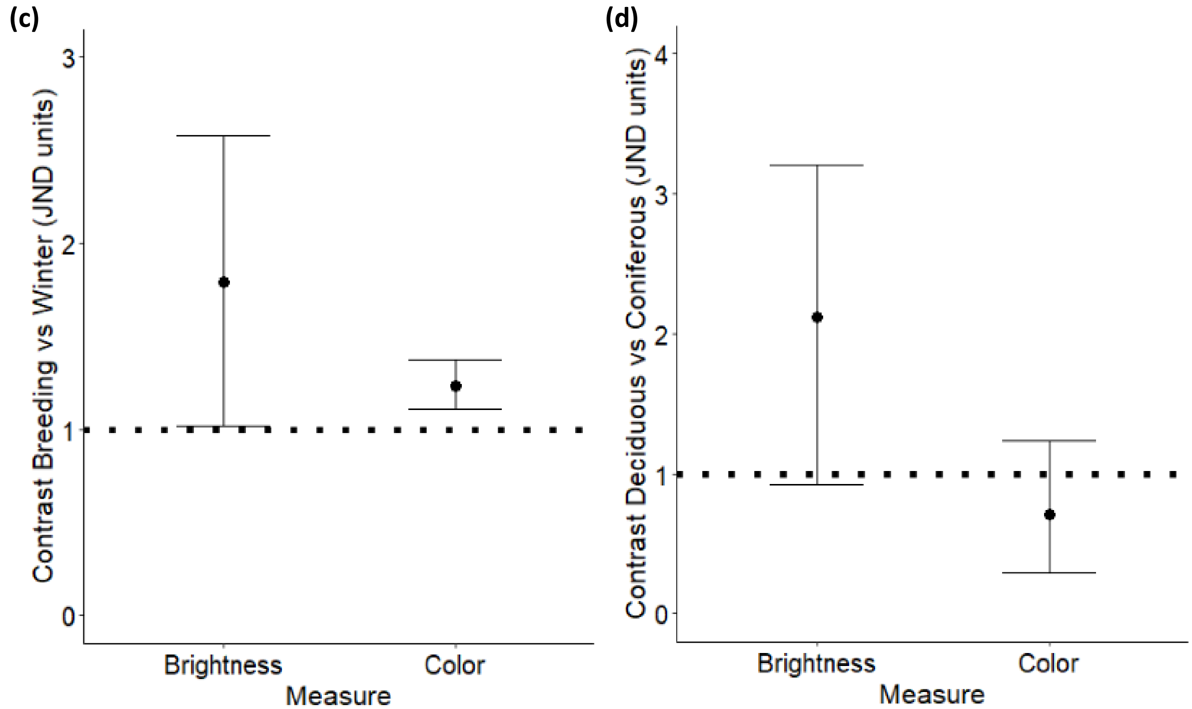
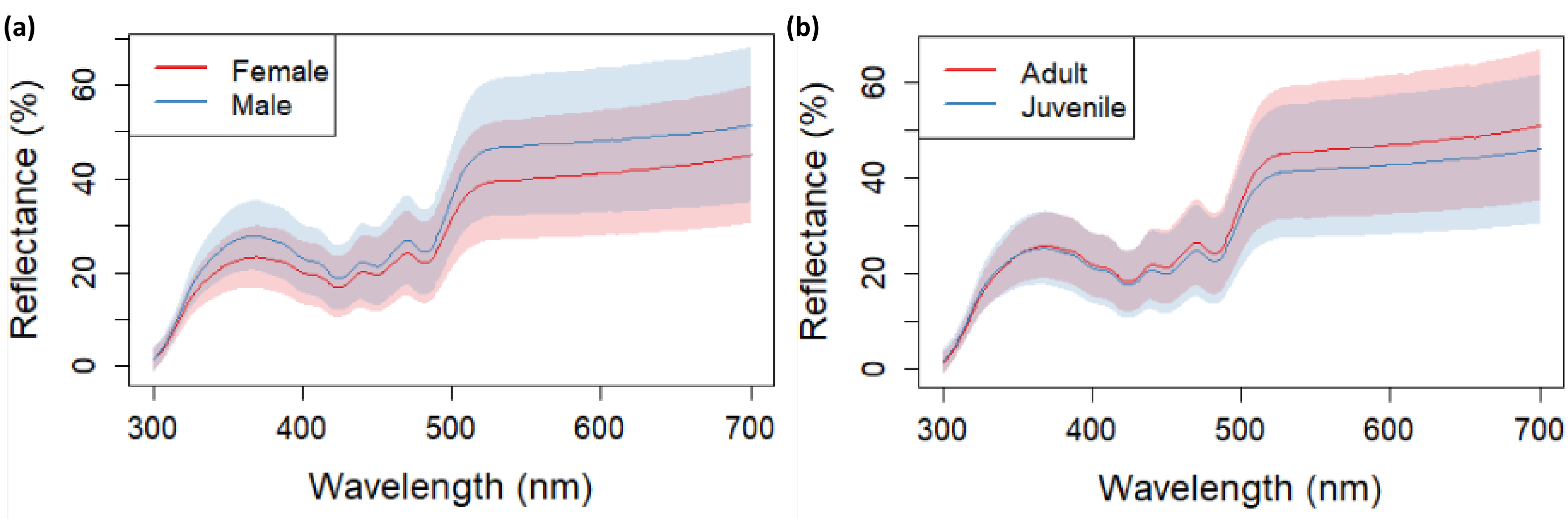



**Figure 3** Just noticeable differences of feather color and feather brightness for Great Tits. Each graph shows the JND values and error bars for the 95% confidence intervals for feather color and brightness. If the JND value does not overlap with 1, then it is predicted that an average Great Tit would be able to see a difference between the feathers of **(a)** males and females, **(b)** juveniles and adults, **(c)** breeding plumage and winter plumage, and **(d)** individuals that live in deciduous and coniferous habitats.

These differences are clearly visible on the average reflectance spectra of males vs females (**Fig. 4a**), adults vs juveniles (**Fig. 4b**), winter vs breeding season (**Fig. 4c**), and coniferous vs deciduous habitats (**Fig. 4c**).



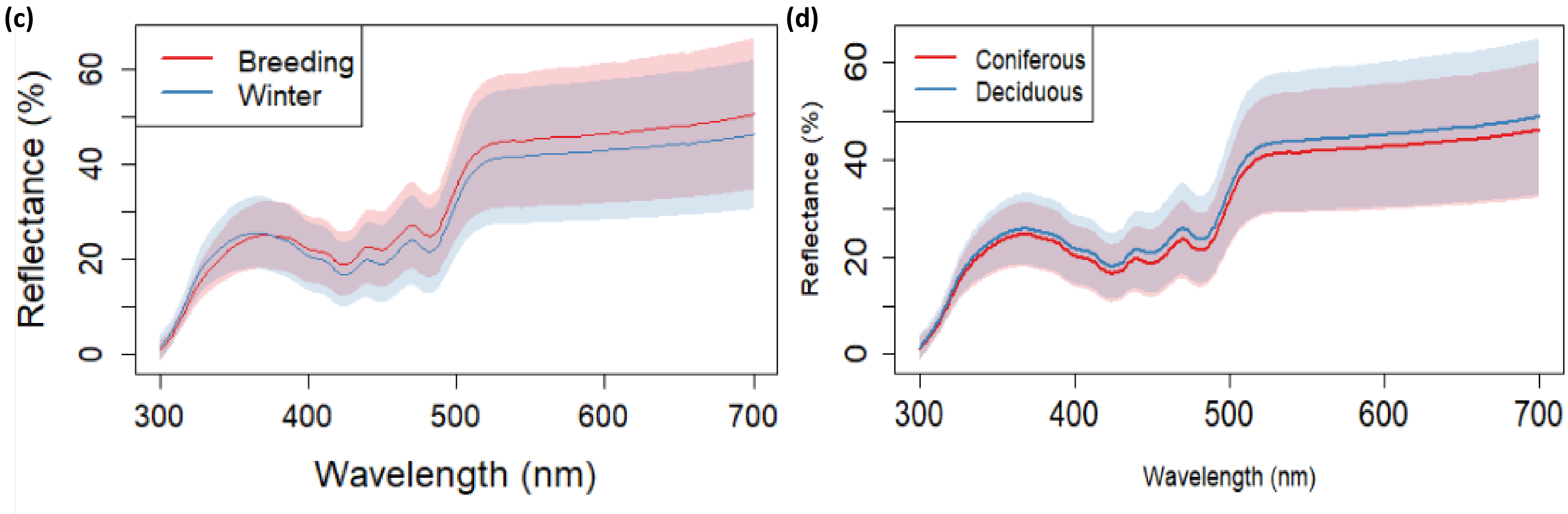



**Figure 4** Reflectance spectra of feather color comparing the average reflectance of breast feathers of **(a)** Males and Females, **(b)** Adults and Juveniles, **(c)** individuals caught during the breeding season and the winter season, and **(d)** individuals from coniferous habitats and deciduous habitats. The solid lines indicate the average spectrum, and the shaded area shows the standard deviation of all of the spectra.

The results of the color model showed that age, season, bill length, skull width, and habitat quality all had significant effects on color PC1, but sex, wing length, tarsus length, and bill depth did not. There was a trend towards a significant effect of head and bill length (**Table 2**). The results of the brightness model showed that sex, tarsus length, bill depth, bill length, head and bill length, and skull width all had significant effects on to feather brightness, but age, wing length, and season did not, and there was a non-significant trend for an effect of habitat quality (**Table 3**).

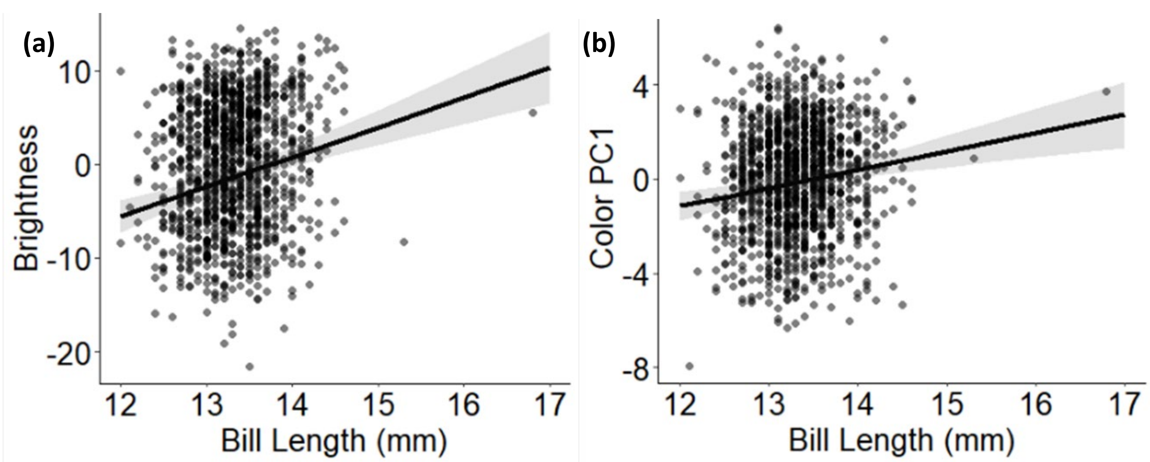
| | **Estimate** | **Std. Error** | **df** | **t-value** | **P-value** |
|---|---|---|---|---|---|
| **(Intercept)** | -1.128e+01 | 5.543e+00 | 7.364e+02 | -2.034 | 0.0423 * |
| **Sex** | 2.806e-01 | 2.124e-01 | 7.376e+02 | 1.321 | 0.1869 |
| **Age** | -8.192e-01 | 1.681e-01 | 1.148e+03 | -4.873 | 1.25e-06 *** |
| **Wing length** | -1.658e-03 | 4.936e-02 | 8.194e+02 | -0.034 | 0.9732 |
| **Tarsus length** | 1.050e-01 | 1.239e-01 | 5.663e+02 | 0.847 | 0.3973 |
| **Season** | 9.816e-01 | 1.601e-01 | 1.165e+03 | 6.133 | 1.18e-09 *** |
| **Bill depth** | -3.437e-01 | 3.815e-01 | 1.076e+03 | -0.901 | 0.3678 |
| **Bill length** | 8.311e-01 | 1.979e-01 | 1.108e+03 | 4.200 | 2.89e-05 *** |
| **Head and bill length** | -3.682e-01 | 1.973e-01 | 8.716e+02 | -1.866 | 0.0623 . |
| **Skull width** | 7.432e-01 | 3.080e-01 | 7.911e+02 | 2.413 | 0.0160 * |
| **Habitat quality** | -3.808e-01 | 1.691e-01 | 3.280e+02 | -2.252 | 0.0250 * |

**Table 2** Outputs of the color model including an estimate value, the standard error (Std. Error), degrees of freedom (df), the t-value, and p-value for the variables sex, age, wing length, tarsus length, season, bill depth, bill length, head and bill length, skull width, and habitat quality. The symbols "***" and "*" indicate that the p-value is significant, with "***" indicating a p-value less than 0.001 and "*" indicating a p-value less than 0.05. The symbol (.) indicates a p-value that is less than 0.1 but this is not considered significant.

| | Estimate | Std. Error | df | t-value | P-value |
|---|---|---|---|---|---|
| **(Intercept)** | 15.7513 | 15.2261 | 734.9659 | 1.034 | 0.301248 |
| **Sex** | 4.5080 | 0.5835 | 735.5889 | 7.726 | 3.65e-14 *** |
| **Age** | -0.5771 | 0.4611 | 1137.6693 | -1.252 | 0.210976 |
| **Wing length** | -0.2227 | 0.1356 | 817.6907 | -1.643 | 0.100741 |
| **Tarsus length** | -1.3115 | 0.3406 | 568.8951 | -3.850 | 0.000131 *** |
| **Season** | -0.3617 | 0.4389 | 1154.2863 | -0.824 | 0.410032 |
| **Bill depth** | -4.8446 | 1.0468 | 1069.0726 | -4.628 | 4.15e-06 *** |
| **Bill length** | 3.1313 | 0.5430 | 1099.3442 | 5.767 | 1.05e-08 *** |
| **Head and bill length** | -1.8664 | 0.5418 | 870.3650 | -3.445 | 0.000598 *** |
| **Skull width** | 4.2148 | 0.8458 | 788.9391 | 4.983 | 7.70e-07 *** |
| **Habitat quality** | 0.8309 | 0.4653 | 334.1681 | 1.786 | 0.075065 . |

**Table 3** Outputs of the brightness model including an estimate value, the standard error (Std. Error), degrees of freedom (df), the t-value, and p-value for the variables sex, age, wing length, tarsus length, season, bill depth, bill length, head and bill length, skull width, and habitat quality. The symbol "***" indicates that the p-value is less than 0.001 and therefore significant. The symbol (.) indicates a p-value that is less than 0.1 but this is not considered significant.

There was a positive relationship between both bill length and feather brightness (p = 1.05e-08) (**Fig. 5a**) and bill length and color PC1 (p = 2.89e-05) (**Fig. 5b**). There was also a positive relationship between skull width and feather brightness (p = 7.70e-07) (**Fig. 5c**) and skull width and color PC1 (p = 0.0160) (**Fig. 5d**).



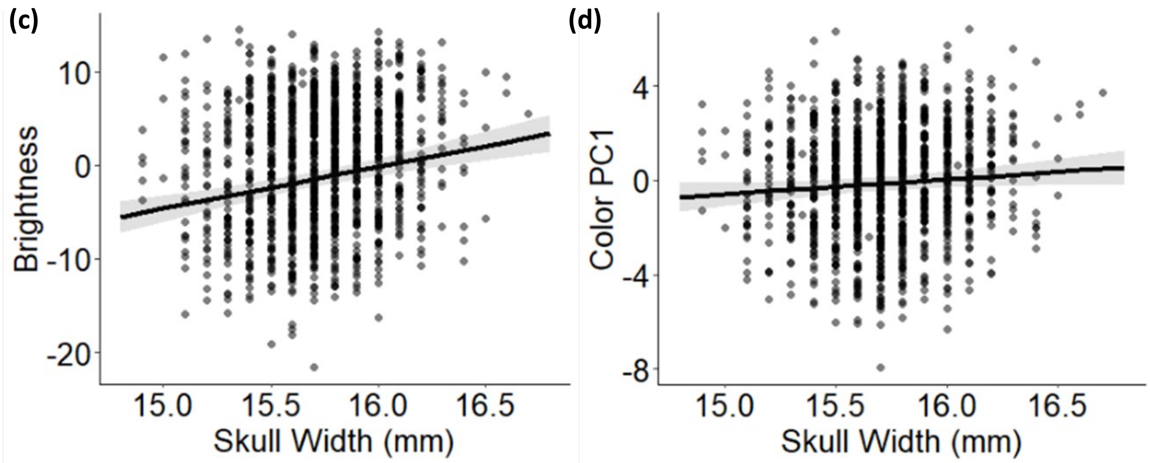



**Figure 5** Significant correlations of skull width and bill length measurements with feather color variables for **(a)** Bill Length and Brightness, **(b)** Bill Length and Color PC1, **(c)** Skull Width and Brightness, and **(d)** Skull Width and Color PC1. Each graph shows plotted points, each point representing an individual sample, with darker points indicating higher density of points, as well as a line of best fit and a 95% confidence interval.

There was no indication from the results that color PC1 is correlated with past reproductive success variables (**Tables 4 & 5**), there was also no relationship between color PC1 and future reproductive success (**Tables 6 & 7**). There was also no indication that brightness is correlated with past reproductive success (**Tables 8 & 9**) or with future reproductive success (**Table 10 & 11**).

| | **Estimate** | **Std. Error** | **df** | **t-value** | **P-value** |
|---|---|---|---|---|---|
| **(Intercept)** | 0.33445 | 0.71957 | 204.85144 | 0.465 | 0.64257 |
| **Past clutch size** | -0.04329 | 0.12674 | 204.61167 | -0.342 | 0.73304 |
| **Sex** | 0.31560 | 0.30699 | 127.45952 | 1.028 | 0.30587 |
| **Age** | 0.87553 | 0.31786 | 204.92372 | 2.754 | 0.00641 ** |

**Table 4** Outputs of the color model including an estimate value, the standard error (Std. Error), degrees of freedom (df), the t-value, and p-value for the variables past clutch size, sex, and age. The symbol "**" indicates that the p-value is less than 0.01 and therefore significant.

| | **Estimate** | **Std. Error** | **df** | **t-value** | **P-value** |
|---|---|---|---|---|---|
| **(Intercept)** | -0.29422 | 0.36993 | 181.55898 | -0.795 | 0.42746 |
| **Past num fledged** | 0.12108 | 0.08487 | 188.82357 | 1.427 | 0.15531 |
| **Sex** | 0.27824 | 0.30337 | 129.08635 | 0.917 | 0.36078 |
| **Age** | 0.90798 | 0.31471 | 205.94192 | 2.885 | 0.00433 ** |

**Table 5** Outputs of the color model including an estimate value, the standard error (Std. Error), degrees of freedom (df), the t-value, and p-value for the variables past number of chicks fledged, sex, and age. The symbol "**" indicates that the p-value is less than 0.01 and therefore significant.

| | Estimate | Std. Error | z-value | P-value |
|---|---|---|---|---|
| **(Intercept)** | 1.752774 | 0.051392 | 34.106 | <2e-16 *** |
| **Color PC1** | 0.005652 | 0.011529 | 0.490 | 0.624 |
| **Sex** | -0.024961 | 0.057565 | -0.434 | 0.665 |
| **Age** | -0.023265 | 0.058098 | -0.400 | 0.689 |

**Table 6** Output of model for predictability of future clutch size, including an estimate value, the standard error (Std. Error), the z-value, and the p-value for the variables color PC1, sex and age. The symbol "***" indicates that the p-value is less than 0.001 and therefore significant.

| | Estimate | Std. Error | z-value | P-value |
|---|---|---|---|---|
| **(Intercept)** | 1.170154 | 0.081910 | 14.286 | <2e-16 *** |
| **Color PC1** | -0.012755 | 0.016038 | -0.795 | 0.426 |
| **Sex** | 0.072702 | 0.087853 | 0.828 | 0.408 |
| **Age** | 0.003618 | 0.083051 | 0.044 | 0.965 |

**Table 7** Output of model for predictability of future number of chicks fledged, including an estimate value, the standard error (Std. Error), the z-value, and the p-value for the variables color PC1, sex and age. The symbol "***" indicates that the p-value is less than 0.001 and therefore significant.

| | Estimate | Std. Error | df | t-value | P-value |
|---|---|---|---|---|---|
| **(Intercept)** | -1.8574 | 2.0730 | 205.0000 | -0.896 | 0.3713 |
| **Past clutch size** | -0.2822 | 0.3648 | 205.0000 | -0.774 | 0.4401 |
| **Sex** | 3.6841 | 0.8522 | 205.0000 | 4.323 | 2.4e-05 *** |
| **Age** | 1.9121 | 0.9168 | 205.0000 | 2.086 | 0.0382 * |

**Table 8** Outputs of the brightness model including an estimate value, the standard error (Std. Error), degrees of freedom (df), the t-value, and p-value for the variables past clutch size, sex, and age. The symbols "***" and "*" indicate that the p-value is significant, with "***" indicating a p-value less than 0.001 and "*" indicating a p-value less than 0.05.

| | Estimate | Std. Error | df | t-value | P-value |
|---|---|---|---|---|---|
| **(Intercept)** | -4.6323 | 1.0500 | 206.0000 | -4.412 | 1.65e-05 *** |
| **Past num fledged** | 0.3814 | 0.2414 | 206.0000 | 1.580 | 0.1157 |
| **Sex** | 3.5744 | 0.8469 | 206.0000 | 4.221 | 3.65e-05 *** |
| **Age** | 1.9952 | 0.9082 | 206.0000 | 2.197 | 0.0291 * |

**Table 9** Outputs of the brightness model including an estimate value, the standard error (Std. Error), degrees of freedom (df), the t-value, and p-value for the variables past number of chicks fledged, sex, and age. The symbols "***" and "*" indicate that the p-value is significant, with "***" indicating a p-value less than 0.001 and "*" indicating a p-value less than 0.05

| | Estimate | Std. Error | z-value | P-value |
|---|---|---|---|---|
| **(Intercept)** | 1.7519299 | 0.0516312 | 33.932 | <2e-16 *** |
| **Brightness** | 0.0002204 | 0.0044116 | 0.050 | 0.960 |
| **Sex** | -0.0241038 | 0.0600680 | -0.401 | 0.688 |
| **Age** | -0.0195042 | 0.0579399 | -0.337 | 0.736 |

**Table 10** Output of model for predictability of future clutch size, including an estimate value, the standard error (Std. Error), the z-value, and the p-value for the variables brightness, sex, and age. The symbol "***" indicates that the p-value is less than 0.001 and therefore significant.

| | Estimate | Std. Error | z-value | P-value |
|---|---|---|---|---|
| **(Intercept)** | 1.158117 | 0.083323 | 13.899 | <2e-16 *** |
| **Brightness** | -0.008104 | 0.006056 | -1.338 | 0.181 |
| **Sex** | 0.102144 | 0.091256 | 1.119 | 0.263 |
| **Age** | -0.010438 | 0.082249 | -0.127 | 0.899 |

**Table 11** Output of model for predictability of future number of chicks fledged, including an estimate value, the standard error (Std. Error), the z-value, and the p-value for the variables brightness, sex and age. The symbol "***" indicates that the p-value is less than 0.001 and therefore significant.

Repeatability

I also found that feather color was not repeatable in this set of data, but brightness was (**Tables 12 & 13**).

| R | SE | CI | P |
|---|---|---|---|
| 0.0475 | 0.0378 | (0, 0.133) | 0.16 |

**Table 12** Output of repeatability estimation for color PC1, including the repeatability estimate (R), the standard error (SE), the Confidence interval (CI) and the likelihood ratio test p-value (P)

| R | SE | CI | P |
|---|---|---|---|
| 0.129 | 0.0437 | (0.0469, 0.218) | 0.002 |

**Table 13** Output of repeatability estimation for brightness, including the repeatability estimate (R), the standard error (SE), the Confidence interval (CI) and the likelihood ratio test p-value (P)

## Discussion

Birds see the world differently than humans do, and it is important to consider this when analyzing the visual aspects of feathers. By using visual models that emulate how a bird would see the feathers I used in this study, I gained a better understanding of what sort of information feather coloration could be communicating to other birds and what variables may influence feather color. To understand how coloration affects the choices and behaviors of birds, we must take into account how a bird sees the world and how they might be processing what they are seeing. We have progressed in our ability to analyze data in a way that better reflects the subject that we are studying (Hill et al. 2006) but is important to also account for how our subjects perceive the world.

My findings that males have brighter feathers than females is consistent with previous findings (Iskasson et al. 2008). This finding, along with the difference in feather coloration during the breeding season supports the hypothesis that feather coloration is at least partially influenced by sexual selection and mating behavior (Hill 1990). However, the lack of correlation between feather coloration and reproductive success variables indicate that if there is a preference for brighter feathers, it does not result in increased offspring production. My results indicate that there is a significant relationship between color and age, as well as a noticeable difference in brightness based on age, which is contradictory to past studies (Hõrak et al. 2001, Iskasson et al. 2008). It is likely that the reason for this difference in coloration is due to the fact that adults have had more molting cycles than juveniles (Fitze et al. 2003).

The numerous correlations between feather coloration and skull and bill measurements could be due to foraging behavior because the type of food a great tit forages is related to their bill morphology (Bosse et al. 2017) which impacts their consumption of carotenoids. The relationship between feather coloration and foraging behavior is further supported by the findings that habitat type is also correlated with feather coloration. Foraging behavior and diet availability could also be an alternative explanation for the seasonal differences of feather coloration, since the carotenoids that contribute to feather coloration are variable in different seasons (Gosler 1987). These findings support the hypothesis that feather coloration could be an indicator of habitat quality.

A limitation of this study has been my methods of analysis. Condensing my data into one variable (color PC1) allowed for easier analysis, but the actual meaning of this variable is abstract and difficult to interpret. It is worth looking into alternative methods of data analysis so that I can interpret results more clearly and definitively.

The correlation between various head and bill measurements with both feather color and brightness supports the idea that bill morphology affects coloration. In addition, given that habitat quality is significantly correlated with color PC1 and almost significantly correlated with brightness, I believe that the next step to understanding these relationships is to analyze the diet of these birds. Diet affects great tit color (Partali et al. 1987) and bill morphology (Gosler 1987), and it would be interesting to see how the observed relationships are affected by this added variable. One such variable is habitat since diet depends on the available resources and some habitats have more resources than others (Mänd et al. 2005).

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