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Morphological and Color Variation in Poicephalus Parrots

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Morphological and Color Variation in *Poicephalus* Parrots

by

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Abstract

Though describing and delimiting species is one of the principle aspects of many disciplines within biology, there is often debate about which methods and concepts should be used to make such decisions. The Tobias criteria for quantitative species delimitation represent one attempt to create a standard method of delimiting species based on the morphological species concept. However, previous examples of using these criteria have not always been completely quantitative. This study uses quantitative morphological and color data of three *Poicephalus* parrots as a case study for the effectiveness of the Tobias criteria. The results show varying levels of support for and dissent against previous species decisions made regarding these parrots, and may provide support for rethinking these past delimitations as well as working towards multifaceted, quantitative decision-making for future species.

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Introduction

In the field of conservation, species classification can have a major impact on the amount of resources that are dedicated to conservation efforts (Mace 2004, Raven and Wilson 1994, Westman 1990). More resources are likely to be invested in conserving an endangered species, rather than one population of a relatively populous species (Joseph *et al.* 2009, Mace 2004, Raven and Wilson 1994, Westman 1990). Because of this, scientists must think carefully about how species are delineated. Methods vary depending on which species concepts are utilized, and these inconsistencies create disagreement across the field of conservation, limiting the ability of conservations to take necessary and timely action (Raven and Wilson 1994).

One of the most widely accepted definition of a species is the biological species concept, which defines species as groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 2000). Therefore, much modern taxonomic decision-making stems from studies of reproductive isolation. However, with the advent of modern technology, taxonomists have also begun to work hand in hand with geneticists as DNA sequencing becomes more accessible. While this can be and has been used reliably to delineate species (Pons *et al.* 2006), it is not always accurate. Because rates of morphological and molecular change may not be equivalent (Bromham *et al.* 2002), differences in DNA sequences may not correlate with significant enough phenotypic differences to create reproductive isolation. In addition, though DNA sequences may or may not be correlated with biologically significant traits that would indicate reproductive isolation, many sequences create phenotypic differences, which are essentially another way of describing morphology. In addition, DNA work regarding gene sequences disregards the effect of regulatory DNA, which can lead to speciation by changing gene expression rather than the genes themselves (Mack *et al.* 2016). Overall, it is necessary to use DNA in tandem with morphology to prevent species delineations from being

described along arbitrary sequence divides with no effect on reproductive isolation (Will *et al.* 2005).

Because of this, morphology is still a valuable option for describing species. Not only is it an inexpensive technique, it can be combined behavioral observations, appropriate DNA evidence, ecological and geographical divides, and more to create a more well-rounded description of a species. One important distinction between historical morphological observations and modern ones, however, is that data should be quantitative, rather than qualitative. The quantitative criteria for species delimitation put forth by Tobias *et al.* (2010) create a way for scientists to describe the difference between species, specifically avian species, using a set list of phenotypic descriptors that can be classified as having exceptional, major, medium, or minor distinctiveness. Scoring plumage, vocal, biometric, and ecological or behavioral characters on this scale can then be used, according to Tobias *et al.*, to determine whether two species should be separate. This technique has been used successfully to analyze the distinction between known separate species and is a good baseline for understanding morphological differences. However, despite making an argument for quantitative measurements, Tobias *et al.* counterintuitively used qualitative analysis of color as a character to score. Qualitative methods include general visual scoring by a researcher and the slightly more standard method of comparing plumage to color swatches (Collar & Fishpool 2017, Wirminghaus *et al.* 2002). Though color measurement devices are less accessible than calipers or rulers, they are becoming more commonly used. Quantitative variables have been defined (Stoddard and Prum 2008) and can be measured and compared to existing literature.

The primary variables utilized to discuss color are hue, chroma, and brilliance. Because avian vision is tetrahedral, Stoddard and Prum (2008) determined a method of quantifying color

geometrically with these variables arranged in a tetrahedron. Hue is equivalent to which color on the spectrum is reflected and therefore seen and is represented in tetrahedral space as a vector of angles θ and Φ between the four color vertices (Stoddard and Prum 2008). Chroma is equivalent to the saturation or intensity of the color and is represented in tetrahedral space as the length of the hue vector (Stoddard and Prum 2008). Brilliance is equivalent to average reflectance, and is measured separately from color as total reflectance divided by the number of reflectance spectra recorded (Stoddard and Prum 2008).

Though the use of tetrahedral space is useful for analyzing avian plumage in particular, another common method of quantifying color variables is the use of three-dimensional color spaces. These originated in 1931 with the CIE XYZ scale, and several others have been developed since that time (Trezona 2001). One such newly developed color space is the HunterLab color scale, which provides three measurements (Hunter L, Hunter a, and Hunter b) as axes for a three-dimensional plot to represent color, in which +100 L indicates white, 0 L indicates black, any positive a indicates red, any negative a indicates green, any positive b is yellow, and any negative b is blue (Whetzel 2015). In this color space, similar colors cluster together based on amount of reflectance spectra detected in the range described by each of the variables (Whetzel 2015).

These standard measurements and calculations for color descriptions provide a way to reliably measure plumage coloration quantitatively. If morphological characteristics are used quantitatively for species studies as per Tobias *et al.*, all traits must be measured in such a way, and these discrete variables allow for the possibility of including plumage into this quantitative analysis.

One group of species to which the Tobias critera have been applied are the Cape parrot (*Poicephalus robustus)*, the brown-necked parrot (*Poicephalus fuscicollis fuscicollis)*, and the grey-headed parrot *(Poicephalus fuscicollis suahelicus)*. These parrots were only recently split into a species and two subspecies (BirdLife International, 2017), having previously all been identified as one species under the name *Poicephalus robustus.* Their species and IUCN Red List statuses have been under much debate (Perrin 2005, Collar & Fishpool 2017), leading to concerns about conservation efforts. Collar and Fishpool (2017) underwent an exhaustive analysis of existing data surrounding the species. They described the various ways in which previous studies lacked quantitative measurements and used biased recording methods. Even after rightfully critiquing most of these previous works, Tobias criteria were employed as part of Collar and Fishpool's decision-making process, and all plumage analyses were completed in a qualitative manner. The plumage in these species identifies sex and age, indicating that it is likely important for reproduction (Wirminghaus *et al.* 2001), so it is not unreasonable to believe that a quantitative description of the plumage would be beneficial to the description of the species. In addition, morphometric measurements did not include standard avian body measurements such as tarsus length (Collar and Fishpool 2017, Muriel *et al.* 2010). The Tobias criteria also do not utilize any statistical analyses, and have been criticized for returning to a purely morphometric species concept, rather than studying morphometrics in conjunction with traits more applicable to the biological species concept (Remsen 2015).

Therefore, quantitative data describing the plumage differences between these species, additional morphometric measurements, and the acknowledgement of the intersectionality necessary in species decision-making may be useful for the most accurate species description and delimitation possible. Though *Poicephalus* parrots are used here as a case study, these

methods may be useful for many other avian species. This study aims to use quantitative methods to understand how appropriate the Tobias criteria are as an assessment of *Poicephalus* species status, and to assess the usefulness of the Tobias criteria in avian conservation overall.

Methods

Morphological and color data were collected at the Natural History Museum in Tring, England over a week-long period in July of 2018. Over the course of the study period, 93 individual parrot specimens were measured: 14 *P. robustus*, 16 *P. f. fuscicollis,* 24 *P. f. suahelicus*, 19 red-fronted parrots (*Poicephalus gulielmi*), and 20 brown-headed parrots (*Poicephalus cryptoxanthus*). *P. gulielmi* and *P. cryptoxanthus* were utilized as morphological outgroups due to morphological similarity of *P. gulielmi* to the focal species despite taxonomic and geographic distance (IUCN 2018), and the morphological difference of *P. cryptoxanthus* to the focal species despite sympatry with *P. f. suahelicus* (IUCN 2018).

Body measurements (Table 1) were collected using a measuring tape and calipers and included wing length, tail length, head height, beak length, beak width, mandible depth, maxilla depth, head width, red forecrown width (if applicable), red forecrown length (if applicable), and tarsus length (Collar and Fishpool 2017, Muriel *et al.* 2010). Color measurements (Table 2) were taken using a tungsten halogen light source set to D65 illumination and an OceanOptics USB 2000+UV-VIS spectrometer with a fiberoptic probe and probe holder, and were taken from the crown, forecrown, cheek, base of the skull, upper back, mid-back, base of the tail, tip of the tail, upper shoulder, lower shoulder, coverts, primaries, throat, breast, belly, leg, and ankle (Figure 1) (Stoddard and Prum 2008, Wirminghaus *et al*. 2001). Data recorded with the spectrometer were X, Y, Z, x, y, z, L, a, b, Hunter L, Hunter a, Hunter b, dominant wavelength, hab hue angle,

chroma, excitation purity, whiteness, Tw tint, u, v, uv saturation, huv hue angle, CIEu, and CIEv (data definitions provided in Appendix 1).

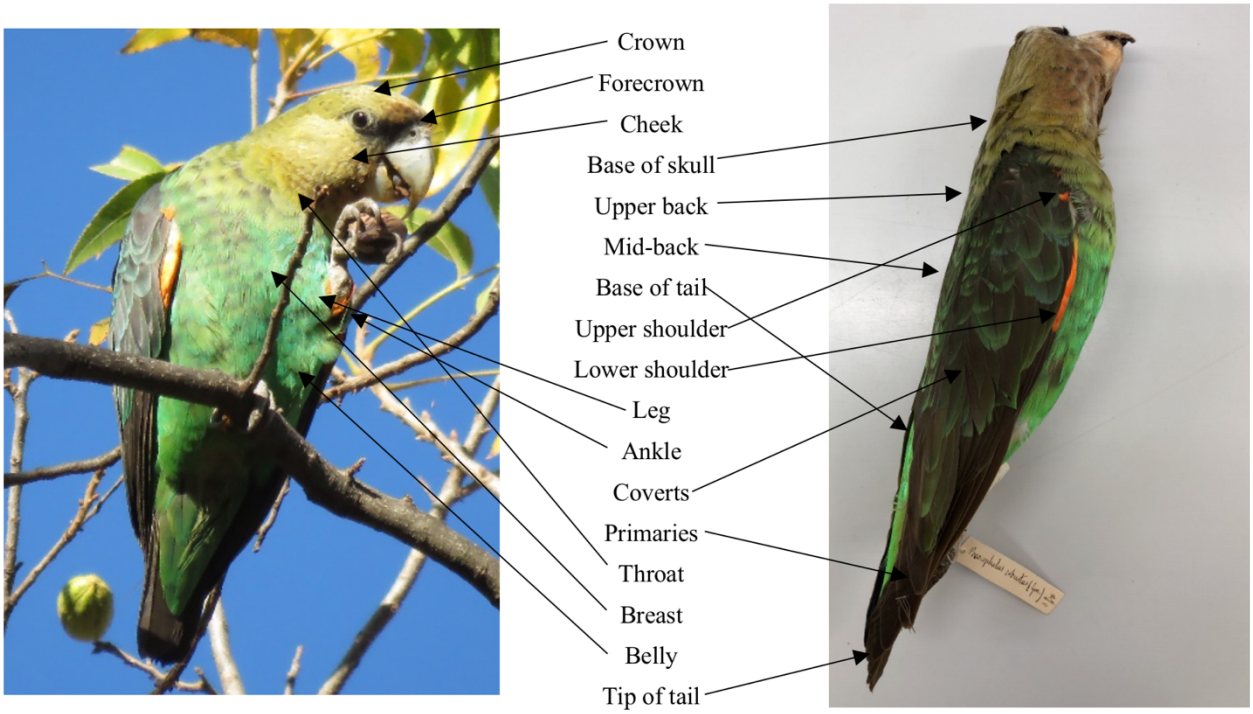

Fig 1. Approximate locations of color patches

Morphological data were analyzed using Multivariate Analysis of Variance (MANOVA) and Discriminant Function Analysis (DFA). Color data were analyzed using Linear Discriminant Analysis (LDA) and MANOVAs. All color data were processed as one group, and then grouped into "body," "head," and "red" categories for more specific analysis. During analysis, some body part measurements (leg, tip of tail) and some spectrometer data (X, Y, Z, x, y, z, whiteness, Tw tint, u, v, uv saturation, huv hue angle, CIEu, and CIEv) were excluded due to incomplete recording, smaller sample size, or likelihood of variation due to measurement conditions. Before analysis, some parrot individuals were also removed from the data set due to incomplete recording. After eliminations, 38 parrots were utilized for color analysis. Initial color analysis

was done via LDAs in R Studio. LDAs found to have distinct groupings (identifiable by eye) were selected for MANOVA analysis. MANOVAs for morphological and color data were further analyzed with Pillai's, Wilks', Hotelling-Lawley, and Roy post-hoc tests for overall significance and Tukey HSD post-hoc tests for between-group significance.

Body Measurement	**Operational Definition**
Wing length	From top of left curve of shoulder to tip of longest left wing feather, curved across middle following feather line (measuring tape to 0.1 cm)
Tail length	From point of insertion to tip- calipers between tail retrices as far as possible to tip of longest intact feather (Collar & Van Grouw personal communication, 2018)
Head height	From the bottom of beak to the peak of the skull
Head width	Across head, immediately behind eyes, perpendicular to head height
Tarsus length	From the outer edge of the inner tibiotarsal articulation to the outer base of most exposed middle toe (Muriel *et al.* 2010)
Beak length	From the center of the bottom of the cere to the tip of the maxilla
Beak width	Across the beak at the point where the maxilla and mandible meet
Mandible depth	From the base of the beak up to the point where the maxilla and mandible meet
Maxilla Depth	From the cere down to the point where the maxilla and mandible meet
Forecrown width	Widest point of red forecrown feathers perpendicular to cere
Forecrown length	Longest point of red forecrown parallel to cere

Table 1. Definitions of body measurements (images provided in Appendix 2)

Color Patch	**Category**	**Operational Definition**
Ankle	Red	Approximate middle of red plumage just above foot on most accessible leg
Base of skull	Head	Center of articulation of skull and vertebrae, or closest section accessible to probe
Base of tail (rump)	Body	Center of dark tail plumage closest to green body plumage (Stoddard and Prum 2008)
Belly	Body	Middle of abdomen below keel (Stoddard and Prum 2008)
Breast	Body	Middle of chest approximately superior to keel (Stoddard and Prum 2008)
Cheek	Head	Middle of side of face, behind beak
Coverts	Body	Approximate middle of wing, above long primaries and avoiding red shoulder patch
Crown	Head	Middle of top of head (Stoddard and Prum 2008)
Forecrown	Red	Red patch of feathers immediately behind cere
Leg	Not grouped	Between insertion of leg into abdomen and red ankle patch
Lower shoulder	Red	Lowest part of red shoulder patch
Mid-back	Body	Center of back, between wings and below shoulders (Stoddard and Prum 2008)
Primaries	Body	Furthest extension of primary feathers
Throat	Head/Body	Immediately below beak (Stoddard and Prum 2008)
Tip of tail	Not grouped	Farthest point of tail feather wide enough for probe
Upper back	Body	Center of back, between shoulders
Upper shoulder	Red	Highest part of red shoulder patch

Table 2. Definitions of color measurements and group categorization (images provided in Appendix 2)

Results

Morphometrics

MANOVA tests and post-hoc tests for Wilks' Lambda indicated that there was significant among-group variance for all five parrots including outgroups, and for the study groups of interest (*P. robustus*, *P. f. fuscicollis*, and *P. f. suahelicus)*. Morphometric variation visualized in Figures 2-4.

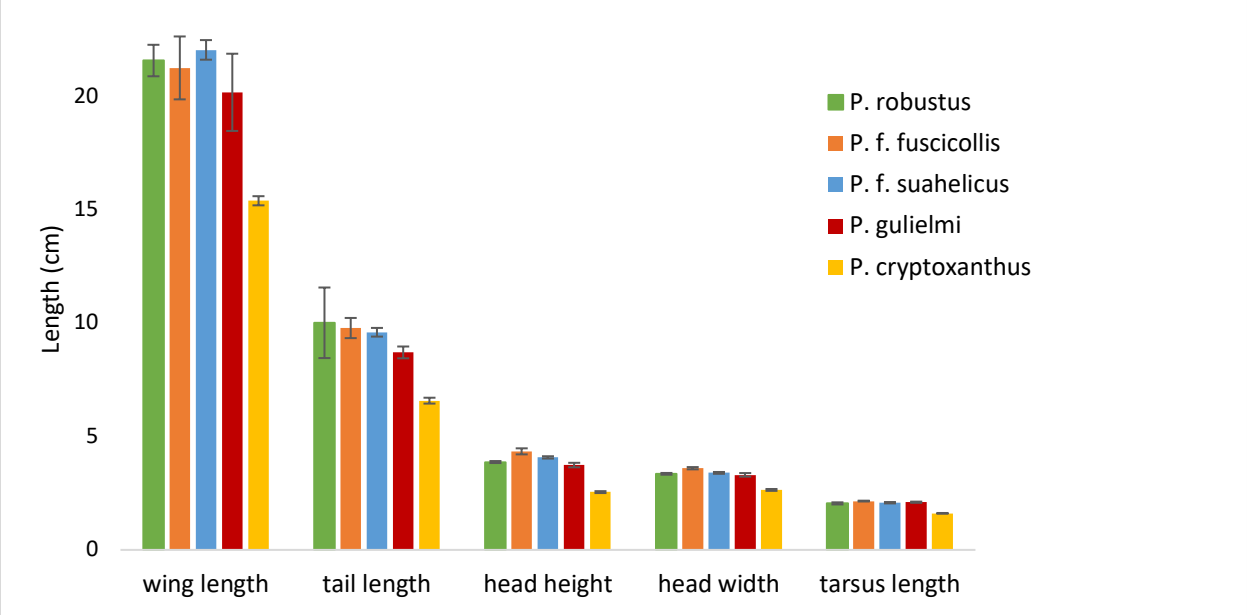

Fig 2. Variation in body morphology of *Poicephalus* parrots. Measurements taken in centimeters. Error bars represent within-group variance.

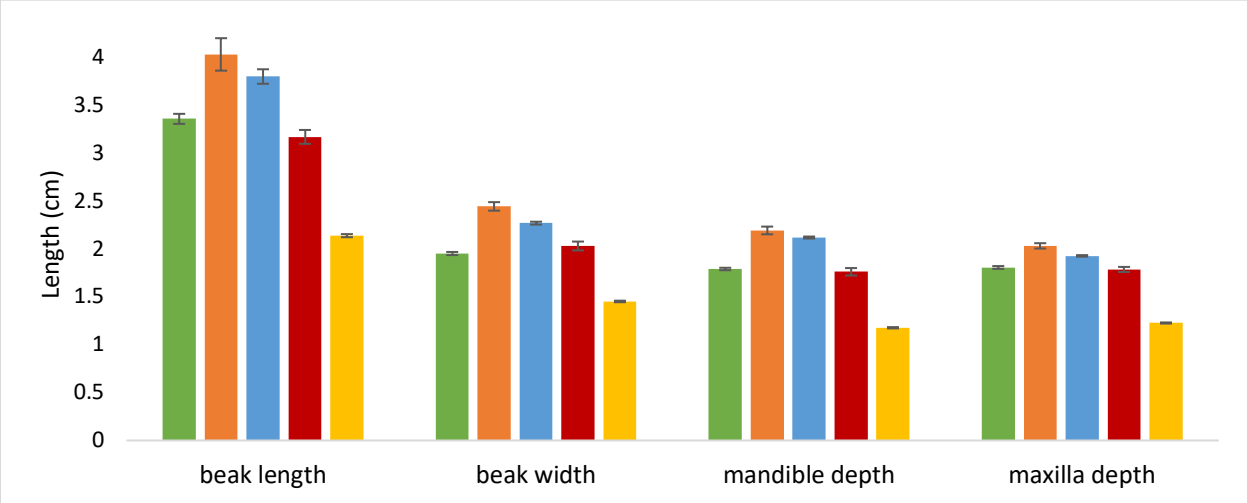

Fig 3. Variation in beak morphology of *Poicephalus* parrots. Measurements taken in centimeters. Error bars represent within-group variance.

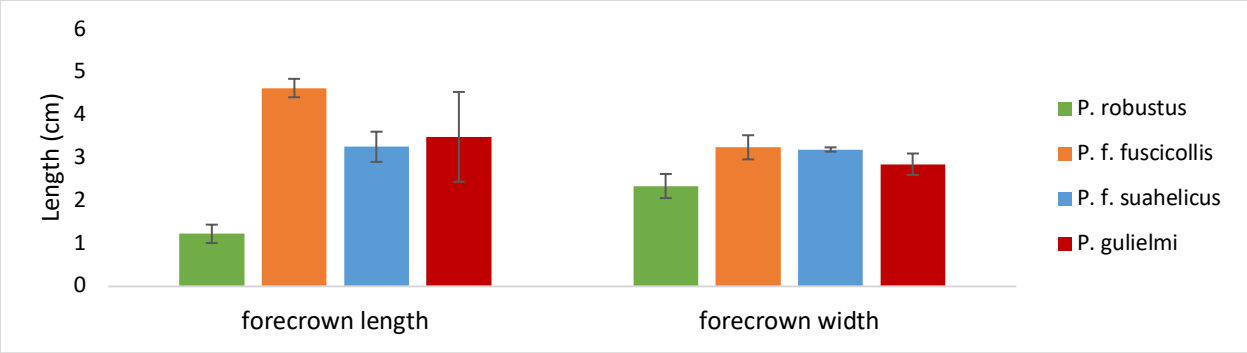

Fig 4. Variation in red forecrown morphology of *Poicephalus* parrots. Measurements taken in centimeters. Error bars represent within-group variance.

These difference were found across the focal species for wing length (MANOVA: F= 6.5701, df= 2, $p < 0.01$), beak length (MANOVA: F= 11.887, df= 2, $p < 0.001$), forecrown length (MANOVA: F= 139.75, df= 2, $p < 0.001$), forecrown width (MANOVA: F= 12.181, df= 2, $p < 0.001$), beak width (MANOVA: F= 37.358, df= 2, $p < 0.001$), mandible depth (MANOVA: F= 30.843, df= 2, $p < 0.001$), and maxilla depth (MANOVA: F= 13.569, df = 2, $p < 0.001$). Post-hoc Tukey HSD test showed that wing length varied significantly between *P. f. fuscicollis* and *P. f. suahelicus* ($p<0.05$), beak length and beak width varied significantly between all pairs ($p<0.05$), forecrown length and forecrown width varied significantly between all pairs ($p<0.05$), mandible depth varied significantly between *P. robustus* and *P. suahelicus* ($p<0.05$), and maxilla depth varied significantly between all pairs ($p<0.05$). Focal parrot morphometric differences visualized in Figures 5-6.

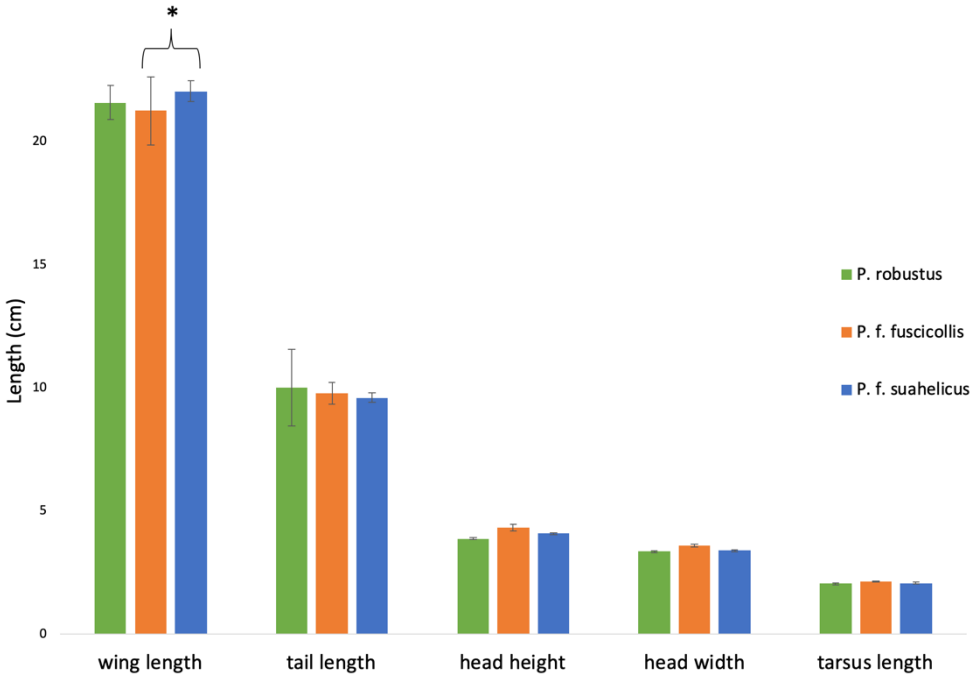

Fig 5. Variation in body morphology of focal *Poicephalus* parrots. Measurements taken in centimeters. Error bars represent within-group variance. * Indicates difference between groups (Tukey HSD, $p<0.05$)

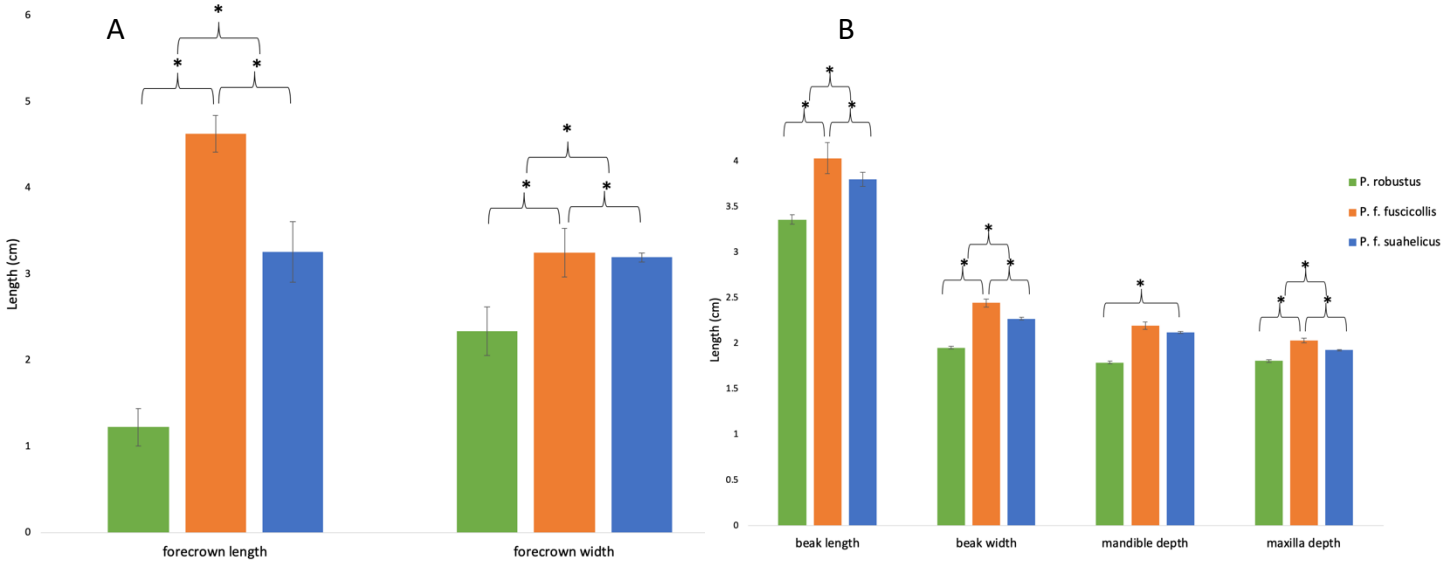

Fig 6. Variation in red forecrown morphology (A) and beak morphology (B) of *Poicephalus* parrots. Measurements taken in centimeters. Error bars represent within-group variance. * Indicates difference between groups (Tukey HSD, $p<0.05$)

Discriminant function analysis (DFA) found that all three focal species are distinctive and that the *P. robustus* is more distinctive from *P. f. fuscicollis* and *P. f.* than *fuscicollis* and *suahelicus* are from each other (Figure 7). The three focal species were correctly classified 89.66% of the time with a Wilks' Lambda (0.1123814) close to 0, indicating a high level of confidence in the results (Figure 8).

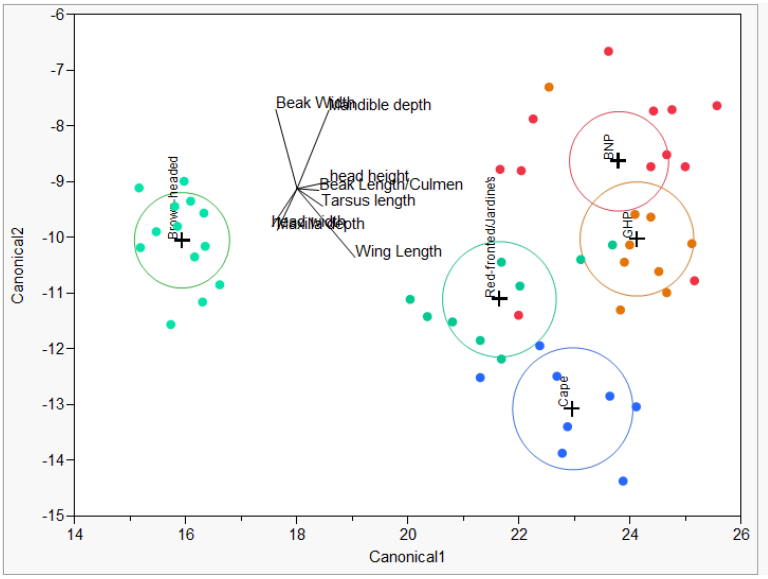

Fig 7. Discriminant function analysis of body measurements of *P. robustus* (blue), *P. f. fuscicollis* (red). *P. f. suahelicus* (orange), *P. gulielmi* (teal), and *P. cryptoxanthus* (green). Wilks' Lambda: 0.0095073 (Prob>F: <.001*); # Misclassified: 4; % Misclassified 7.843.

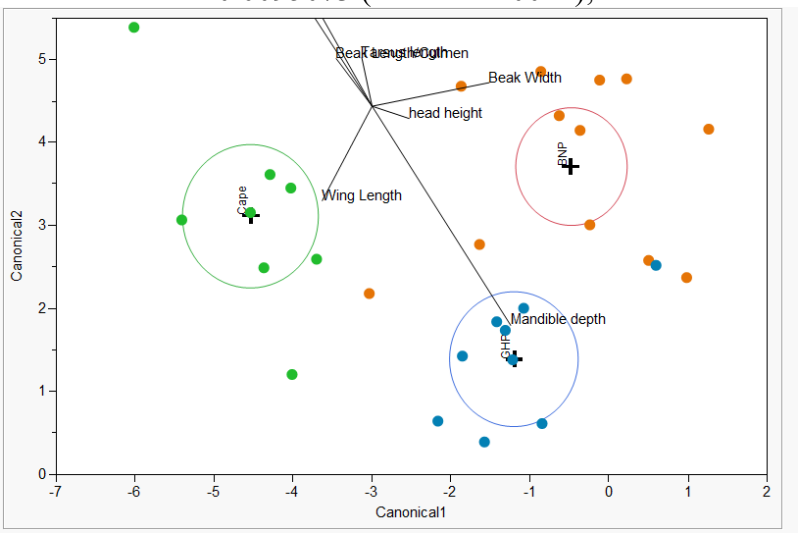

Fig 8. Discriminant function analysis of body measurements of *P. robustus* (green), *P. f. fuscicollis* (orange), and *P. f. suahelicus* (blue). Wilks' Lambda: 0.1123814 (Prob>F: <0.001*); Number Misclassified: 3; % Misclassified: 10.34

Color

Initial LDAs found discrimination between groups (Figures 9-15, additional in Appendix 3). Color measurement comparisons found to have significant differences between species were body L a b (MANOVA: F=2.7074, df=2, p<.001), body Hunter L a b (MANOVA: F=2.8166, df=2, p<0.001), head L a b (MANOVA: F=3.6283, df=2, p<0.001), and head Hunter L a b (MANOVA: F=3.306, df=2, p<0.001). Within these general groups, variables for certain color patches were more significant than others. For the body measurements, belly (a), breast (a, b, Hunter b), coverts (a, b, Hunter a, Hunter b), and primaries (Hunter a) were the most significant (p<0.01 or p<0.001) among all groups. For the head measurements, base of skull (a, b, Hunter a, and Hunter b), cheek (L, a, b, Hunter L, Hunter a, and Hunter b), crown (a, b, and Hunter b), and throat (b and Hunter b) were all significant (p<0.01 or p<0.001) among all groups. Tukey post-hoc tests indicated significance between only *P. robustus* and *P. f. fuscicollis* for Base of skull a, b, Hunter a, and Hunter b; Belly a; Breast a, b, and Hunter b; Cheek a, b, and Hunter b; Crown a, b, and Hunter b; and Throat b and Hunter b (p<0.05). Significance was shown between only *P. f. fuscicollis* and *P. f. suahelicus* for Cheek L and Hunter L; Coverts a; Crown b and Hunter b; and Primaries Hunter a (p<0.05). Significance was shown between only *P. f. suahelicus* and *P. robustus* for Base of skull a, b, Hunter a, and Hunter b; Cheek b, Hunter a, and Hunter b; Coverts b, Hunter a, and Hunter b; Crown a; and Throat b and Hb (p<0.05).

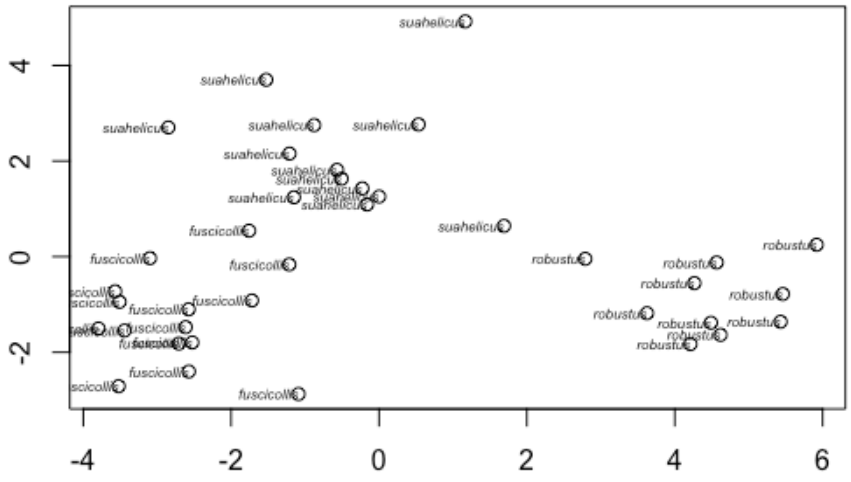

Fig 9. Linear discriminant analysis of body, head, and red color measurements; all variable values. Wilks' lambda: -5.7635e-170 (Prob>F: <.05*)

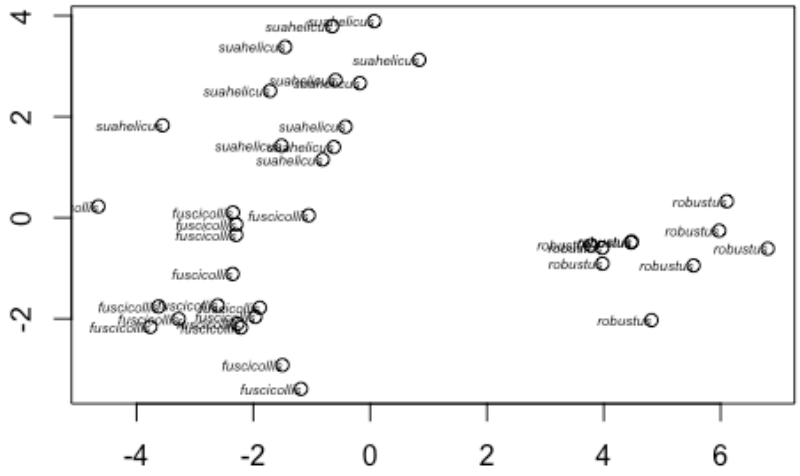

Fig 10. Linear discriminant analysis of body color measurements; L, a, and b values. Wilks' lambda: 0.021792 (Prob>F: <.05*)

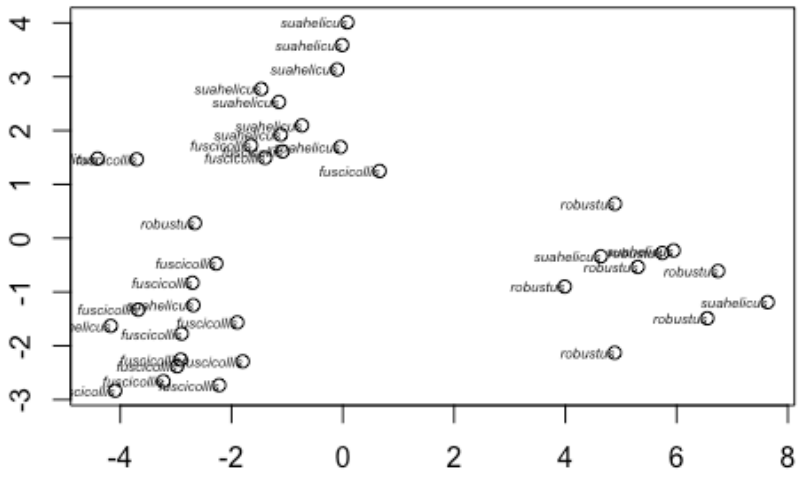

Fig 11. Linear discriminant analysis of body color measurements; Hunter L, Hunter a, and Hunter b values. Wilks' lambda: 0.017798 (Prob>F: <.001*)

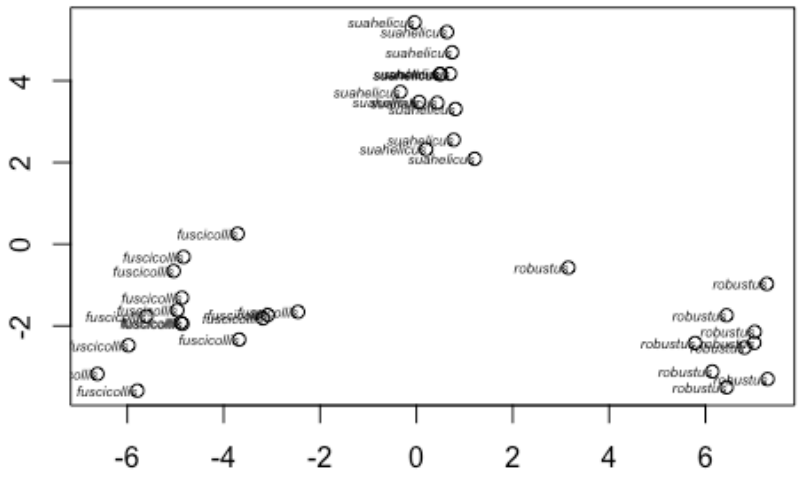

Fig 12. Linear discriminant analysis of head color measurements; all variable values. Wilks' lambda: 3.6581e-28 (Prob>F: <.05*)

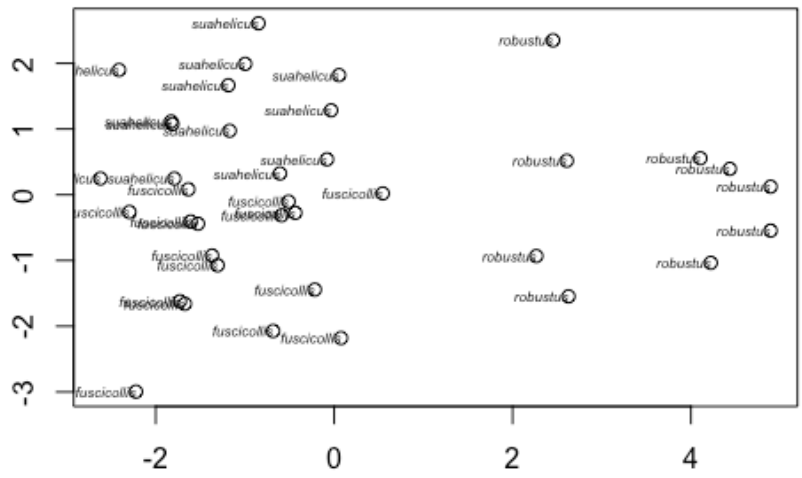

Fig 13. Linear discriminant analysis of head color measurements; L, a, and b values. Wilks' lambda: 0.10286 (Prob>F: <.05*)

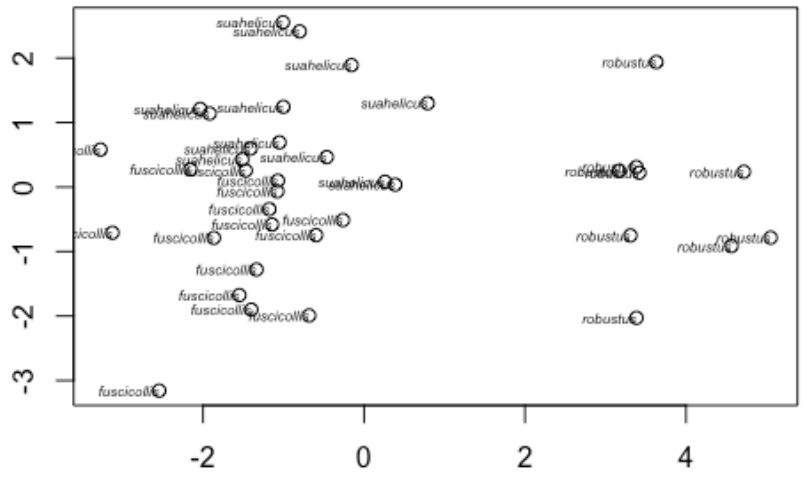

Fig 14. Linear discriminant analysis of head color measurements; Hunter L, Hunter a, and Hunter b values. Wilks' lambda: 0.10334 (Prob>F: <.001*)

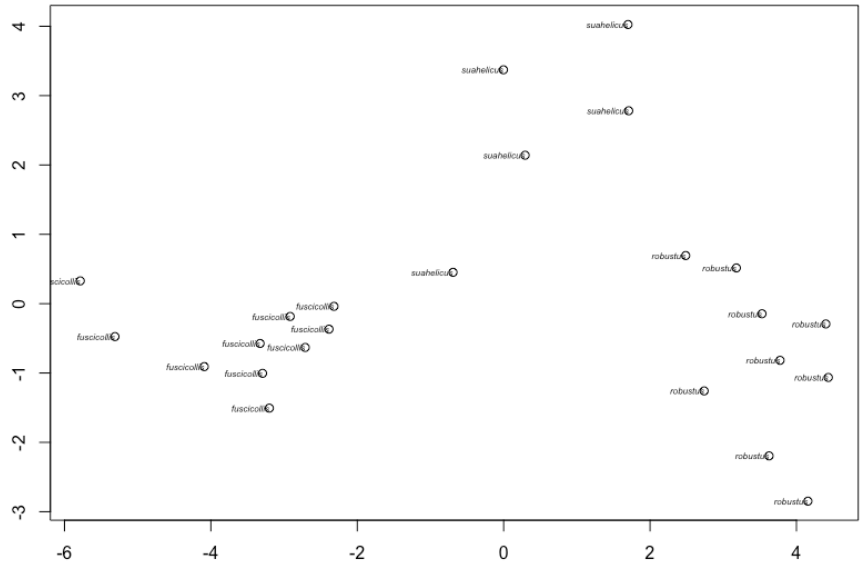

Fig 15. Linear discriminant analysis of red color measurements; all variables. Wilks' lambda: 1.9855e-37 (Prob>F: <.05*)

Discussion

Overall, the morphological traits measured that were found to be significantly different between the three focal species were wing size, several different metrics of beak size, and the length and width of the red forecrown (in applicable species). While collecting data, it was seen that wing size was one of the most regularly measurable indicators of overall body size in the study skins utilized due to inconsistency in stuffing. The significance found indicates that overall body size may be one of the main traits separating these species, which may require sampling live specimens in the future to get accurate data for support. Wing size was also the only variable found to be statistically significant between only *P. f. fuscicollis* and *P. f. suahelicus,* meaning that they are more different from each other than either is from *P. robustus* in that case; this is in contrast with previous work (Collar & Fishpool 2017). Significant differences in the red forecrown width and length across the three species may signal the importance of sexual

dimorphism and/or sexual selection in the species, as the red coloration is an indicator of age and sex in the three focal species.

The results of the morphology DFA could concur with current species delineations that list the Cape parrot as an individual species, while the brown-necked and grey-headed parrots are subspecies (Collar & Fishpool 2017), as the centroids for *P. f. fuscicollis* and *P. f. suahelicus* were closer together than either was to the centroid of *P. robustus*, though all cluster discretely within the 95% confidence intervals.

The results of the color data vary between tests. The LDAs of all of the measurements as well as the L a b and Hunter L a b of the body measurements would also concur with current species delineations (Collar & Fishpool 2017), while the LDA for all head measurements may indicate the potential for a full species split between *P. f. fuscicollis* and *P. f. suahelicus.* In further analysis, the MANOVA and Tukey HSD post-hoc showed significant differences between *P. robustus* and *P. f. fuscicollis* for 16 variables, between *P. f. fuscicollis* and *P. f. suahelicus* for 6 variables, and between *P. f. suahelicus* and *P. robustus* for 13 variables, once again providing potential support for current delineations. Past work has used head color differences as a major part of taxonomic decisions (Collar & Fishpool 2017, Perrin 2005, Wirminghaus *et al.* 2002), and this is beneficial quantitative reinforcement for such studies.

Due to difficulty of access to many of the red color patches, the data for describing them is mostly inconclusive. In addition, a smaller sample size for those patches because of the sexual dimorphism of these parrots made it difficult to draw firm conclusions.

It is to be expected that a study conducted on wild-caught specimens would generate slightly different results than what has been found from these study skins. Handling over the years has led to inevitable wear and tear, such as fraying and even breaking of prominent

primaries and tail feathers, which may have made some measurements slightly inaccurate. In addition, some body measurements were difficult to take due to the posture of the study skins (i.e. tarsus length). Despite this concern, because the data were collected as consistently as possible, and major outliers (completely absent tail feathers, etc) were eliminated in data analysis, the degree of confidence in these results is still high. The age of the specimens may also raise concerns of color fading. However, it has been found that feather pigments do not fade appreciably with age, in the visible or ultraviolet spectra (Armenta *et al.* 2008). Any other systematic error in the color measurements may have stemmed from inconsistent probe handling. However, the data that was most significant for many of the color patches was a, b, Hunter a, and Hunter b, which are empirical measurements of color and do not change with variations in ambient light. These also correspond the most of any of the recorded variables to the color that is perceived by the eye, which would reasonably make them the most important in discussing

Though these data agree somewhat with the current *Poicephalus* delimitation, these phenetic traits in no way represent a complete understanding of these species. To make a complete taxonomic decision regarding these parrots, this morphological and color data should be combined with other criteria, including analysis of vocals, behavioral and ecological traits, and geographic range (Remsen 2015, Remsen 2016). Rather than selecting an individual species concept (i.e. morphological, biological), it is reasonable to use a consolidated species concept (Quaedvlieg *et al.* 2014) which combines as many as possible to create a well-rounded idea of the species delimitation.

The use of the Tobias criteria for quantitative species delimitation in the case of the *Poicephalus* parrots is a case in which the conclusions reached are taxonomically sensible, but this does not mean that these criteria will always be so useful for other cases. The lack of

specificity in the Tobias criteria regarding biologically relevant as opposed to simply morphologically distinct traits means that they could be used to make species decisions that would refute the biological species concept (Remsen 2015). In addition, truly quantitative decisions made in the future will require statistical analysis to determine the magnitude and significance of differences between the species, rather than relying on a somewhat arbitrary character scoring system (Donegan 2018).

This is not to say that these criteria are entirely useless; rather, they can be improved by requiring precise choice of the morphometric traits utilized to make sense in the concept of wider species definitions, and by fulfilling their initial promise of quantitative data for all criteria. In that case, the Tobias criteria could easily be used as a valuable part of a multi-faceted species concept. The impact of taxonomic decisions on species conservation is great enough to warrant great care in making them (Mace 2004). Using an individual method of defining a species is too limiting to be widely applicable across the realm of conservation, which uses species-level biodiversity as a guiding force for all levels of work, from planning to action (Mace 2004).

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Appendix 1- Spectral data definitions

X Y Z, x y z	Three dimensional definition of color in CIE color space, wherein Y (y) represents luminance, Z (z) is related to blue, and X (x) is equivalent to a range of non-negative values that represent the remainder of the visual spectrum (Smith & Guild 1931, Trezona 2001)
L a b, HunterL Huntera Hunterb	Three dimensional definition of color in CIE color space, wherein +100 L (Hunter L) indicates white, 0 L indicates black, any positive a (Hunter a) indicates red, any negative a indicates green, any positive b (Hunter b) is yellow, and any negative b is blue (Whetzel 2015).
Dominant wavelength	Wavelength at which reflectance spectra peaks. In absence of significant peak, average wavelength. (Smith & Guild 1931)
Hab hue angle	Inverse tangent of the product of a and b (Hunter a and Hunter b), indicating angle between the two colors in the CIE color space (Smith & Guild 1931)
Chroma	Saturation (intensity) of color, indicated by amount of reflectance in spectral range of color of interest (Stoddard and Prum 2008)
Excitation purity	Placement of color in color space related to dominant wavelength color and achromatic origin (Stoddard and Prum 2008)
whiteness	Degree to which a color is white (reflects all wavelengths) (Smith & Guild 1931)
Tw tint	Degree to which a color appears green (positive value) or red (negative value) (Smith & Guild 1931)
u v, CIEu CIEv	Three dimensional definition of color in CIE color space, with variable definitions similar to x y z space. Able to be transformed to x y z space. (Smith & Guild 1931)
Huv hue angle	Inverse tangent of the product of u and v (CIEu and CIEv), indicating angle between the two colors in the CIE color space (Smith & Guild 1931)
uv saturation	Chroma in the uv wavelength range (<400 nm) (Smith & Guild 1931)

Appendix 2- Color and Body Measurements Methods

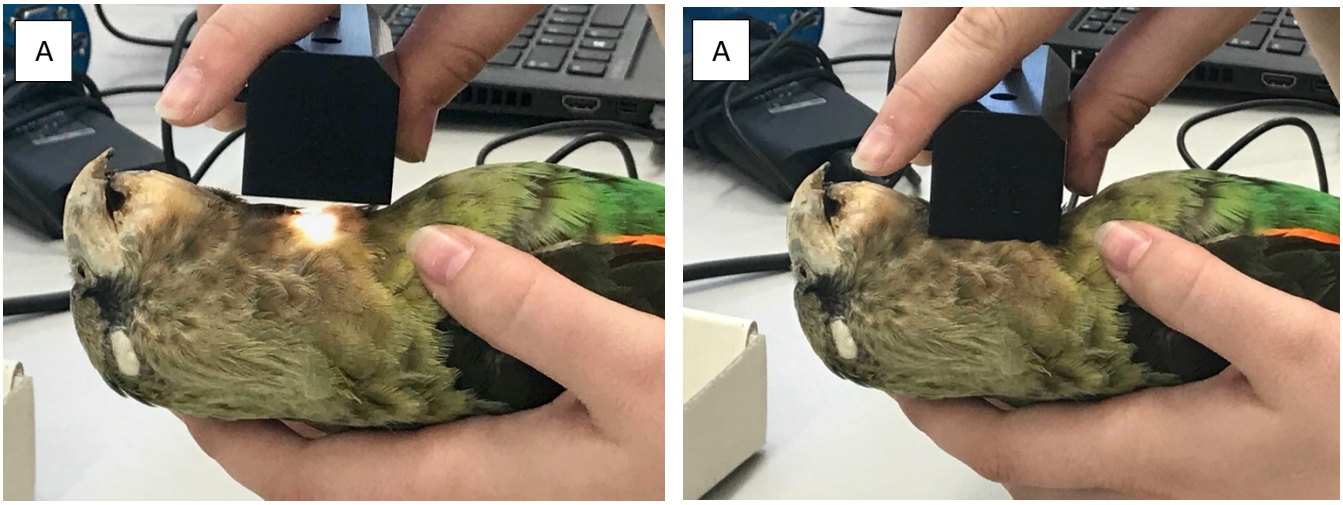


Fig A1. Methods for taking color measurements of plumage- example measurement of *P. robustus* throat (A).

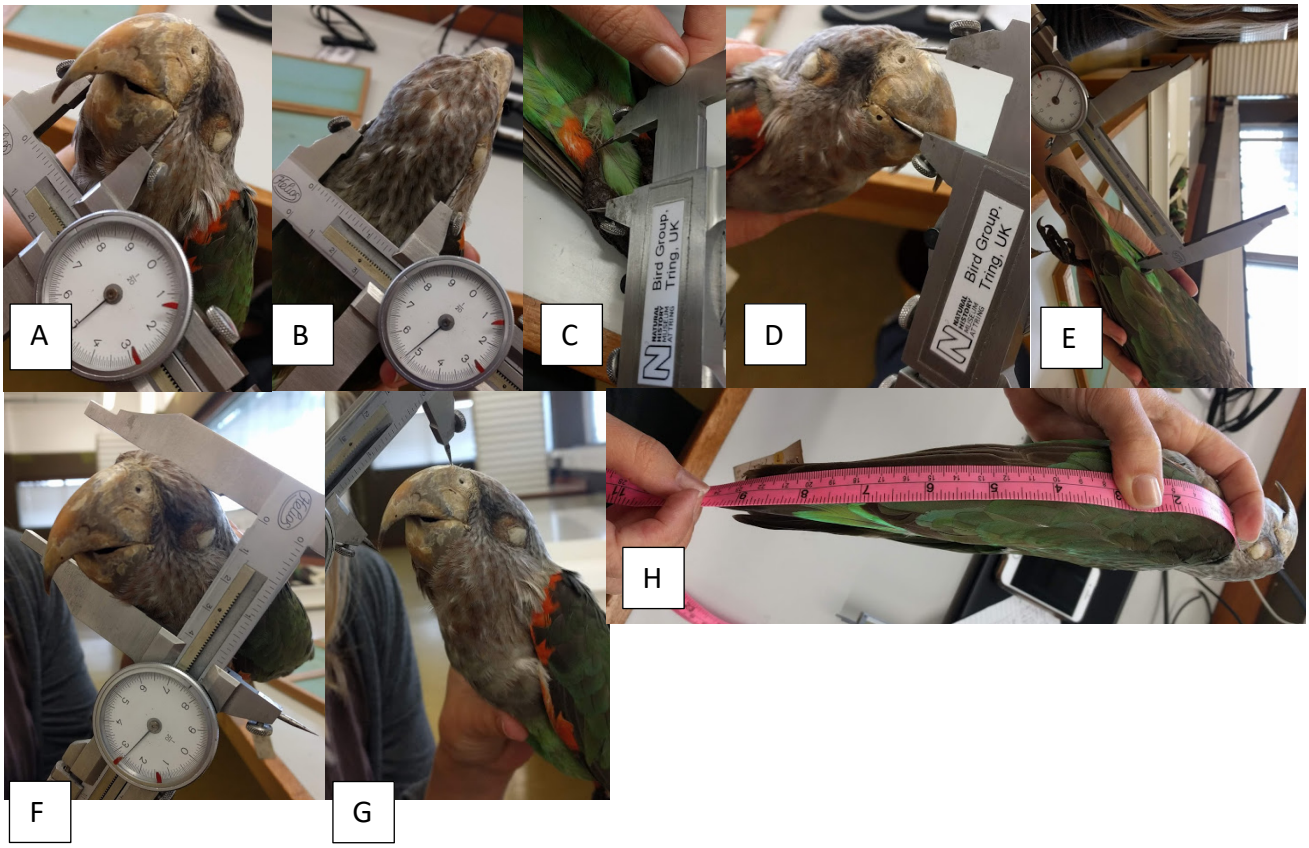
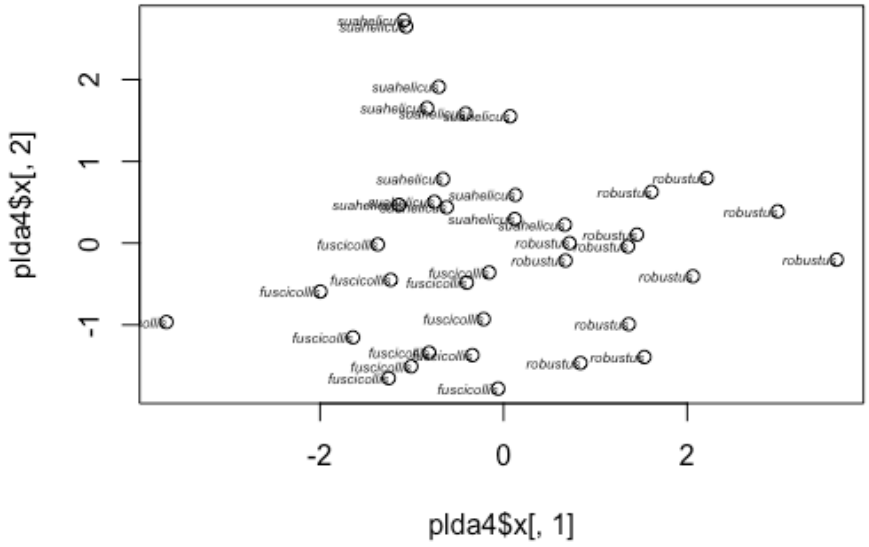
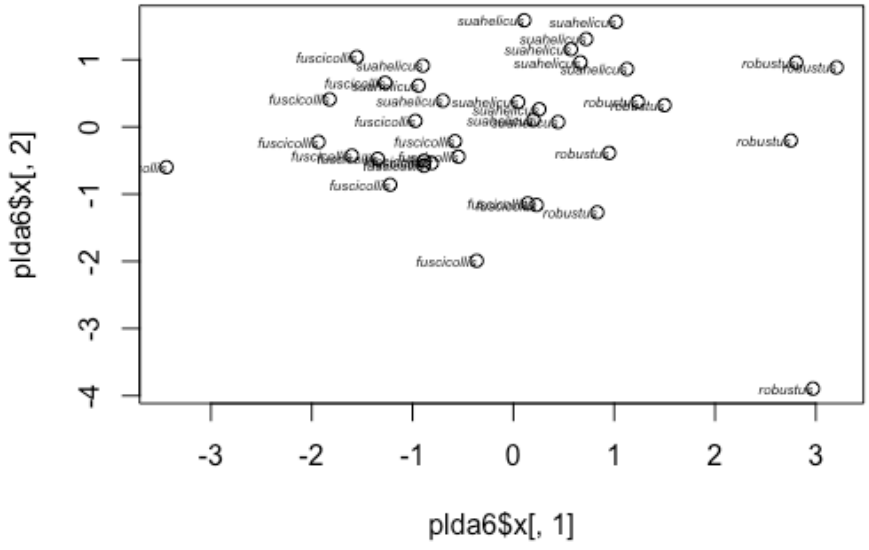


Fig A2. Examples of body measurements of *P. f. suahelicus.* (A) Beak width, (B) Head width, (C) Tarsus length, (D) Maxilla depth, (E) Tail length, (F) Head height, (G) Beak length, (H) Wing length.

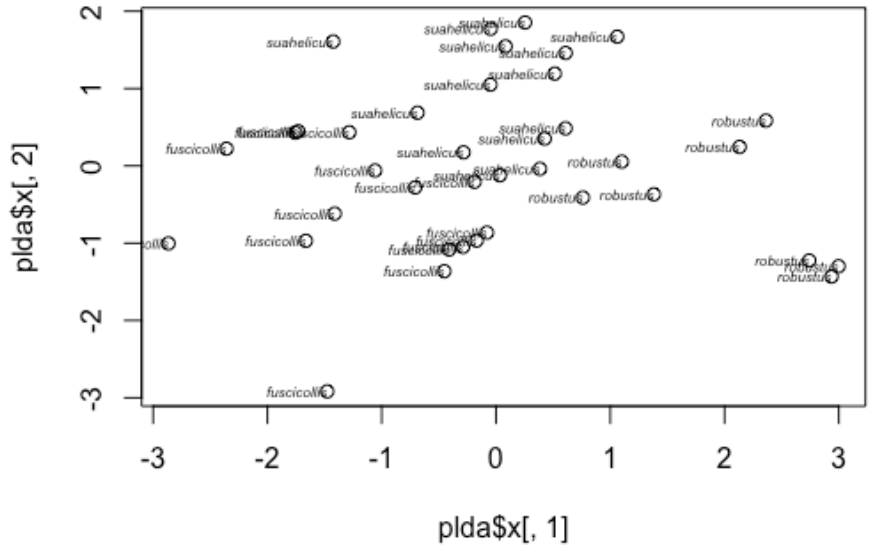
Appendix 3- Additional Linear Discriminant Analyses



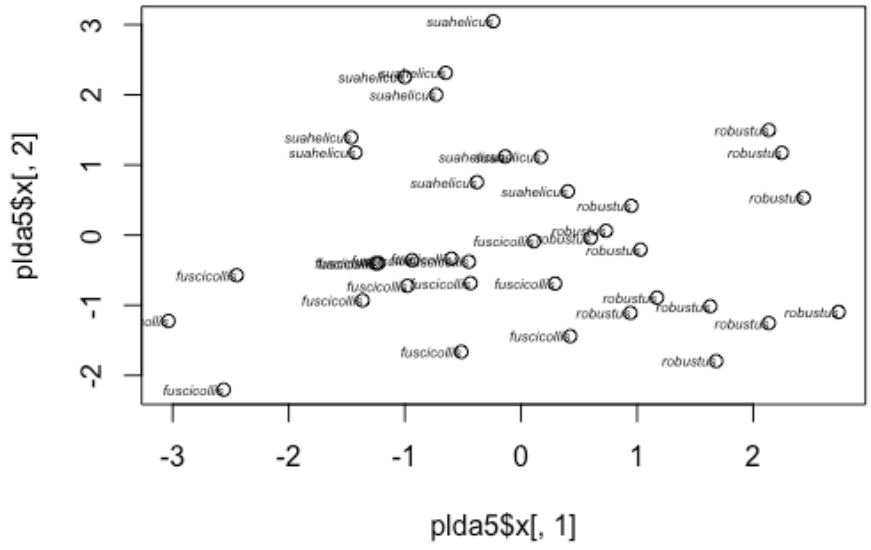
Body chroma



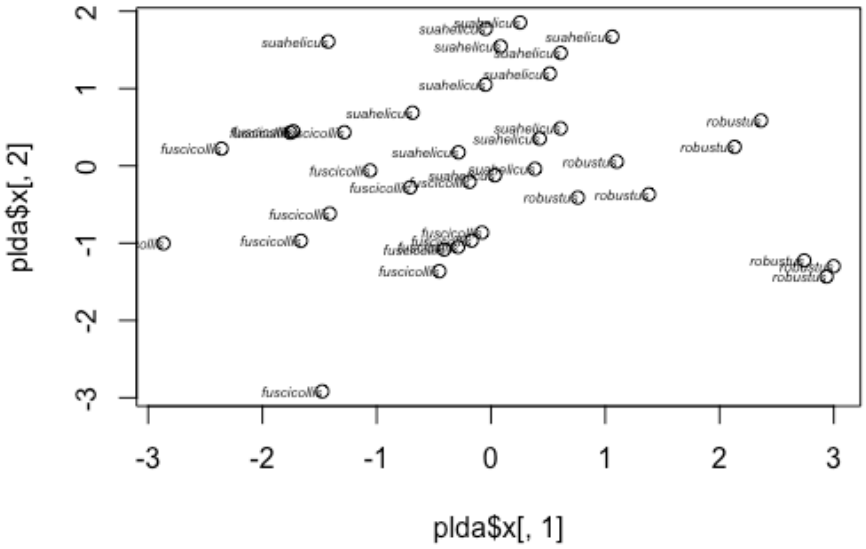
Body hab hue angle



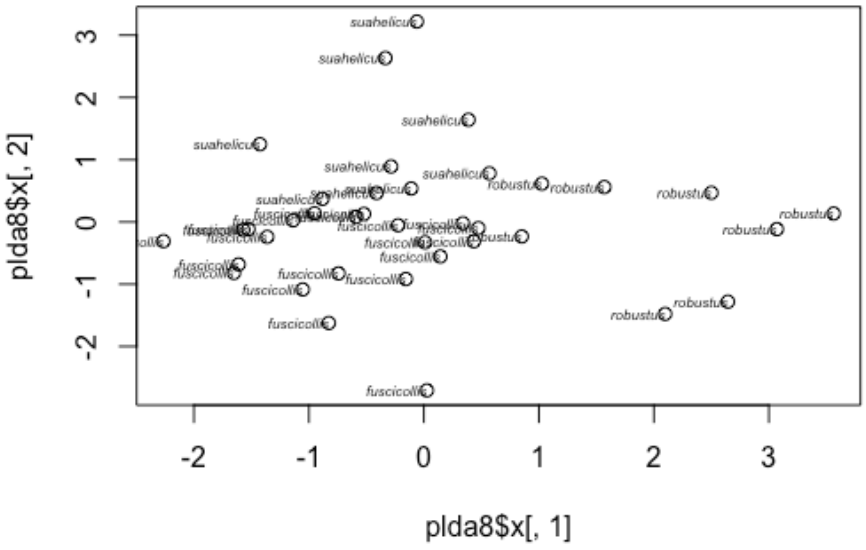
Body color overall



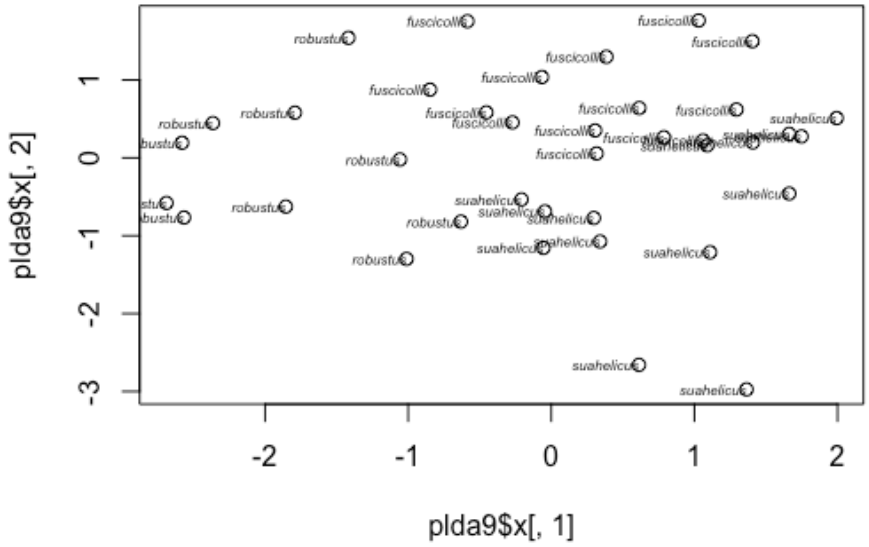
Body excitation purity



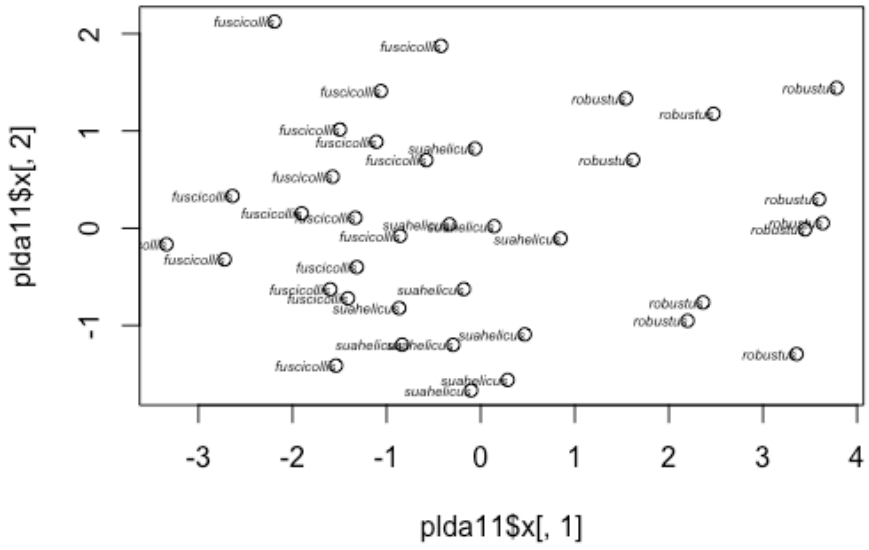
Body dominant wavelength



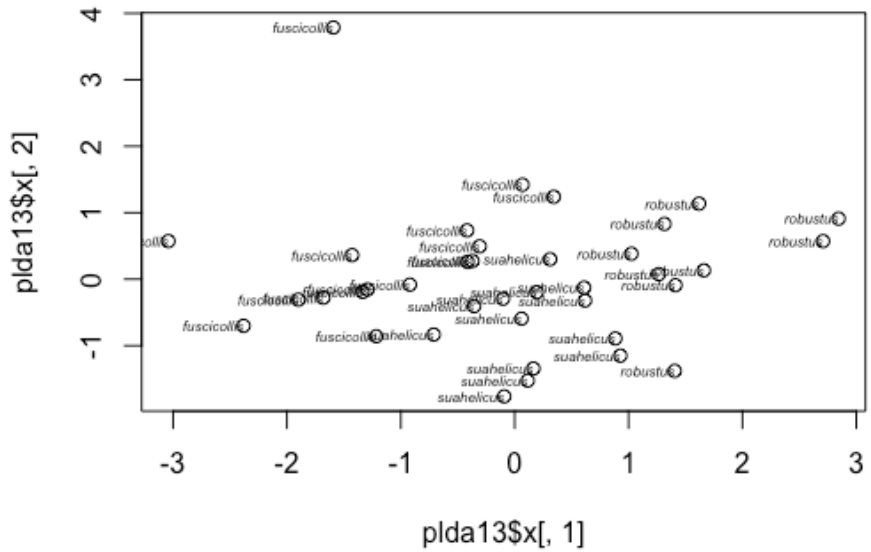
Head chroma



Head excitation purity



Head hab hue angle



Head dominant wavelength