Title
Differential effects of urbanization on plumage and morphometric traits in two congeneric desert cardinal species

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Abstract
Urbanization has greatly affected wildlife over the last century and will continue to do so into the future, but we know very little about whether traits of closely related species respond similarly to this environmental change. This limits our understanding of the environmental stressors that species face in the city. To address this gap, we tested the association between urbanization and several morphological traits of two congeneric species, northern cardinals (*Cardinalis cardinalis*) and pyrrhuloxia (*C. sinuatus*), across the Sonoran Desert city of Tucson, Arizona over the past 137 years. We used both museum and field-collected specimens and applied a novel method to score urbanization over time. We found that urbanization affected carotenoid-based traits, but with different effects on different traits and sexes in each species. For melanin-based plumage traits, urbanization was only associated with less saturated breast plumage in female pyrrhuloxia. Both urbanization and time of sampling were associated with shifts in traits that could allow for improved maneuverability, and with wider bills in males. Our findings demonstrate that urbanization has complex effects on traits involved in signaling, heat tolerance, foraging, and maneuverability. The effects of urbanization can differ even in closely related species that largely share a niche.

Introduction

Human activities have altered ecosystems globally, with only 23.2% of the terrestrial landscape (Watson et al. 2016) and 13.2% of the ocean still classified as wilderness (Jones et al. 2016), and with most wilderness areas under threat of global human impacts such as climate change, pollution, and habitat loss (Asamoah 2022). The impacts of urbanization on community structures have been extensively studied (Beissinger and Osborne 1982, Green 2003, Hostetler and Knowles-Yanex 2003, Litteral and Wu 2012, Hensley et al. 2019, Palacio 2020, Tryjanowski 2020, Brown et al. 2022, Haight et al. 2023), but the effects of this ecological disruption on the phenotypic traits of native species over time are less understood. Broad comparative studies at the community level can reveal overall trends in species abundance and distribution, such as the finding that bird species that persist in the city have a broader environmental tolerance than their rural congeners (Bonier et al. 2007). However, studies of traits from different populations or between closely related species can reveal the fine-scale mechanisms underlying these differences (i.e Kern and Langerhans 2018, Winchell et al. 2018). This gap in our understanding highlights the urgent need for research on a diversity of morphological traits in response to urbanization.

Commented [1]: cite Jeff's nature paper comparing ecological communities across multiple urban areas using camera traps when it comes out

Urban landscapes reshape selective pressures and environmental conditions for birds in a number of documented ways (Badyaev et al. 2008, Brown and Brown 2013, Hutton and McGraw 2016, Giraudeau et al 2014, McNew et al. 2017), and urbanization often removes correlations between color signals and behaviors or survival in birds (reviewed in Sepp et al. 2020). Urban stressors can be chemical pollution, noise, artificial light at night, human presence, novel patterns of resource distributions (reviewed in Isaksson 2018), and novel assemblages or abundances of species including pathogens (Giraudeau et al. 2014, Jiménez-Peñuela et al. 2019). Phenotypic differences across urban gradients can indicate which of these stressors have affected species, and therefore indicate which stressors might limit or shape urban patterns of species richness (Isaksson 2018). For instance, plumage color associated with a reduction in carotenoids can result from chemical pollution (Isaksson et al. 2005) or novel assemblages of plant species (Isaksson and Andersson 2007) but plumage color associated with an increase in carotenoids can result from invasive species that are rich in carotenoids (Jones et al. 2010). Bill shape can be made longer and narrower due to reliance on anthropogenic food sources in bird feeders (Giraudeau et al. 2014) or shorter and wider due to increased competition and species interactions (Badyaev et al. 2008). And traits associated with maneuverability can be selected for as well, such as an increased need for quick, deft movements associated with longer tails and shorter wings (Brown and Brown 2013). While studies of phenotypic changes across an urban area can illuminate the stressors affecting species, we do not know if the traits of sympatric congeners respond similarly to the same stressors in the same environment. Slight differences in congeneric species' responses to the same stressors could reveal mechanisms of adaptation associated with urbanization.

Population- and individual-level urban bird studies most often focus on the same species (e.g. house finches *Haemorhous mexicanus*, great tits *Parus major*; Heinen-Kay et al. 2021), and sample birds over short time frames, often less than 30 years (Fidino and Magel 2018). This limits our understanding of the consistency of trends across species, and of the responses of species over long-term urbanization. To develop a more comprehensive framework for the impacts of human activities on species, new research methods that integrate species comparisons with sampling schemes across many decades are needed. Museum collections offer the ability to compare phenotypes across time, as plumage and morphometric traits remain measurable across decades with proper methods (Burns et al. 2017). Despite this, they have only rarely been used to analyze urban impacts on species over time, with only 12% of urban evolution studies accessing museum specimens (Shultz et al. 2021), and of those only one analyzed a species' phenotype over time in both urban and rural populations, rather than just in urban areas (Snell-Rood and Wick 2013).

Northern cardinals have recently emerged as a novel study system for understanding effects of urbanization on plumage color and trait sizes. Studies of the nominate subspecies (*Cardinalis cardinalis cardinalis*), which is distributed throughout the eastern United States, have shown effects of urbanization on plumage coloration and body condition (Baldassarre et al. 2022) as well as song (Narango and Rodewald 2016). The northern cardinal is widespread throughout North America, with four genetic populations on the mainland of the continent that span urbanized areas (Smith et al. 2011). The second most predominant subspecies in the United States, *Cardinalis cardinalis igneus*, shares much of its range with its congener, the pyrrhuloxia (*Cardinalis cardinalis sinuatus*; Smith et al. 2011); both are found throughout the Sonoran Desert and in the greater metropolis area of Tucson, Arizona.

The two species are easily distinguished by coloration (Figure 1), with male northern cardinals predominantly red with a black face mask and orange bill, male pyrrhuloxia predominantly gray with a red breast, face mask, crest, shoulder, and tail and orange bill, and females of both species similar to the coloration of the male pyrrhuloxia but with a buffy breast, black mask, and red-orange bill (female northern cardinal), or a gray breast and black mask (female pyrrhuloxia). The plumage of northern cardinals has been shown to have inter- and intra-sexual functions, although with variation between populations (Wolfenbarger 1999, Jawor et al. 2003, Jawor et al. 2004, Jawor and Brietwisch 2004, Jawor and Brietwisch 2006, Rodewald et al. 2011, Winters and Jawor 2017). Pyrrhuloxia also have a "parrotlike" curved bill, while northern cardinals have a more conical bill. Both species come to feeders in Tucson and generally occupy a similar niche with no observed differences aside from a slight preference for proximity to water in northern cardinals (Gould 1961), and little is known about their diet in the Sonoran Desert population (although see McAtee 1908). Northern cardinals are also present more in the urban center of Tucson than Pyrrhuloxia (unpublished data, or Jackson and McGraw 2023 *depending on timing of publication*). These slight differences in phenotype and ecology allow for a unique comparative study of urbanization on traits. Differences in the responses between these species of plumage, bill morphology, wing length, and tail length to urbanization could reveal which environmental stressors limit pyrrhuloxia's urban distribution more than that of northern cardinals and could highlight fine-scale differences in the mechanisms of urban adaptation between even closely related species.

We sought to determine if and how urbanization may affect the plumage and morphometric traits of northern cardinals and pyrrhuloxia. We present findings from morphological traits of northern cardinals and pyrrhuloxia measured across 137 years between urban, urban outskirt, and rural areas across the state of Arizona. We model differences across urban areas to identify traits that have been impacted by human activities, as defined by proximity to urban areas. We expected to find that, if the effects of urbanization are consistent on similar species despite slight differences in ecological niche, the same traits would be impacted in similar ways by urbanization between these species. However, if urbanization differentially impacts closely related species, either the same traits would be affected but in different ways, or different traits altogether would be impacted by urbanization.

Methods

Data collection and processing

For the field portion of this study, we captured and sampled 13 northern cardinals and 12 pyrrhuloxia at Tucson residences from March to May of 2021 and 2022 using a mist net at feeders with black oil sunflower seed. We also took measurements from birds of both species from the University of Arizona's Bird Collection and from the University of Washington's Burke Museum of Natural History and Culture (Table S1), which together hold the majority of museum specimens collected in the state of Arizona and recorded in VertNet (Constable et al. 2010). We limited these to adult specimens collected in Arizona that were associated with reliable location data. We sampled 24 northern cardinals and 39 pyrrhuloxia from UAZ, and 11 northern cardinals and 5 pyrrhuloxia from UWBM, for a total of 48 northern cardinals (39 males and 9 females) and 56 pyrrhuloxia (34 males and 22 females) across both field and museum collections (Figure S1).

Integumentary coloration was quantified using standard digital photography methods that have been validated in other carotenoid-colored passerine species (Giraudeau et al. 2012, Lendvai et al. 2013, McGraw et al. 2002). Our photographic methods did not capture variation in the ultraviolet (UV) portion of the spectrum, but UV and yellow-red reflectances are correlated in carotenoid-based plumages (Senar and Quesada 2006) and previous cardinal color studies have excluded UV (Jawor and Breitwisch 2004). We took photographs with a Canon Rebel T3i and a Kodak color standard of two regions of each bird: their breast and their face in profile (Figure 1). We also photographed underwing plumage of the field specimens because this trait has been shown to vary with urbanization in female northern cardinals from New York (Baldassarre et al. 2022), but we could not evaluate underwing coloration of museum specimens due to the method of preservation. All photographs are available in our Dryad repository for other researchers to access (LINK).

Field photographs were taken in the shade under diffuse sunlight conditions to minimize shadow, and included an 8" Tiffen Color Separation Guide with Grey Scale. Museum photographs were taken in front of a window with color standards to best replicate the natural sunlight conditions of the field samples within the constraints in place by the museums to preserve the specimen. From all field and museum specimens, we also measured length of the crest, wing, and tail to the nearest 1 mm with a wing rule. We measured the longest erect crest feather and the middle of the tail. We also measured tarsus length as well as bill length and width at the nares and head length to the nearest 0.1 mm with analog calipers.

Photographs were analyzed using Photoshop (24.0.1). We analyzed the bill, crest, and face mask of each bird from photographs of the bird's head in profile, and the breast from a separate photo of that region of the bird. We obtained hue, saturation, and brightness values from each patch and from the red square of the Tiffen Color Separation Guide following methods from Giraudeu et al. (2012), except for the mask which is a gray-black shade and thus lacks a spectral peak from which to obtain hue. To standardize our measurements across light environments, we subtracted the value obtained from the Tiffen Color Separation Guide red standard from the value of the trait of interest. All methods were repeated on a second photo of each bird; intraclass correlation coefficients (ICC) were calculated to assess repeatability, and then values were averaged between the two photographs. ICC values ranged from 0.79 to 1.00, with a mean of 0.91 (Table S14).

Measuring the extent of urban impact

Dates for estimating degree of habitat urbanization for the capture locations of the cardinals ranged from 1885-2022, and the urban areas across Arizona changed drastically in size over those 137 years. To our knowledge, no studies have used long-term datasets to model urbanization of wild birds across over a century of samples, so we developed a novel protocol to measure urbanization here. We used a long-term dataset of urban extent, which contains raster files of hindcast modeled urban extents by decade (1880-1990), models from satellite nighttime light by year (1996-2009), or projected future urban sprawl (2020) (Li et al. 2021). The model for 2020 projected urban areas based on past data, rather than on data from 2020, and it modeled urban extents under five different human development scenarios. Despite this, no difference was observed for our sampling locations between the different models. For each raster of urban extent, we generated a new raster file consisting of plots of the same resolution but where each cell represents the Euclidean distance (in m) of that cell to the nearest urban area in the original raster file in R. We then extracted this number from the cell at the same location as each bird-capture location within the raster file of the most recent year that predated the year of capture to generate a “Distance from Urban Area” score for each individual. If latitude and longitude data were not listed for certain museum specimens but there was a reliable description of capture location, i.e. “2.6 mi. E. of Arivaca, Pima Co., Arizona,” then estimates of latitude and longitude were obtained using Google Maps. This attributed an urbanization score ranging from 0 meters (most urban) to 191,634 meters (most rural) to each specimen. Though this effectively captured variation in urbanization at the low end of the range (specimens at 0 meters were similarly all highly impacted by urbanization), cardinals caught at sites without any human development had wide ranging scores. To account for this, we binned the urbanization scores into three categories: Urban (Distance from Urban Area = 0 meters), Urban Outskirts (0 meters < Distance from Urban Area < 12,000 meters), and Rural (12,000 meters < Distance from Urban Area). We chose 12,000 as the cutoff because this was a natural break in our dataset, with no specimen having a distance to an urban area between 11,655 and 32,597 meters, and because all samples in this range appear to fit within the assigned categories when plotted on a map (Figure S2). Analyses of females of both species lacked the sample size to retain these three urbanization categories, so for just the females of each species we lumped “Urban” with “Urban Outskirts” to create two categories: “Urban and Urban Outskirts” and “Rural.” Human activity has increased over time in all areas, not just in urban areas, and museum specimen coloration might decay over time (Armetana et al. 2008). To account for this, we included the year of specimen collection in the model counting backwards with 2022 as year 0. For color traits, it is not possible to disentangle the effects of specimen decay from the effects of change over time on a population, but for morphological characteristics that are based on trait size (i.e. bill length), which should not decay, we inferred that the effects of year on that trait are a result of population change rather than specimen decay.

Data analyses

Dataframes were manipulated prior to analyses in Python using the packages pandas and numpy, and spatial files were processed in R with the packages raster (Hijmans), rgdal (Bivand et al. 2015), and terra (Hijmans et al. 2022). All analyses were run in R with the packages afex (Singmann et al. 2015), car (Fox et al. 2012), effects (Fox and Weisberg 2018, 2019), emmeans (Lenth et al. 2018), FNN (Beygelzimer et al. 2015), Hmisc (Harrell and Harrell 2019), HSAUR (Everitt et al. 2017), interactions (Long 2019), jtools (Long and Long 2017), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017), MASS (Venables and Ripley 2002), and tidyr (Wickham and Wickham 2017). Figures were plotted in R with ggbiplot (Vu, n.d.) and ggplot2 (Wickham et al. 2016).

We tested each morphological variable for normality using a Shapiro-Wilk test, and many were significantly not normal, so we then assessed correlations between all morphological variables by calculating the Spearman correlation coefficient for each pair of variables and the associated p-value. We ran a principal component analysis on the correlation table and repeated this analysis for the color morphological traits and the non-color morphological traits. A high number of variables were significantly correlated with each other (Tables S2-S13). Many of the length variables were significantly intercorrelated for male northern cardinals (Table S2), but none were correlated in male pyrrhuloxia (Table S8). Fewer length variables were intercorrelated for female northern cardinals (Table S5) than for male northern cardinals, and only crest and tail length were correlated in female pyrrhuloxia (Table S11). Color traits in female pyrrhuloxia were highly intercorrelated with each other and only rarely correlated with length variables. Northern cardinal males had the most intercorrelated traits of the four sex and species subgroups. Given the lack of consistent intercorrelation between species and sex groups, models based on the PCs of the variables would prevent any comparison between groups. Similarly, the correlation of any two traits may suggest that they respond similarly to physiological stresses but would not necessarily mean that in the disrupted urban environment that these traits would remain correlated. Therefore, we chose to model each trait rather than the PCs of the traits despite these intercorrelations, as an understanding of the effect of urbanization on each trait is biologically meaningful and statistically appropriate since we model each trait separately.

Color variables for males of either species or for female pyrrhuloxia did not significantly relate to degree of habitat urbanization (Figures S4-S7). They did cluster with some overlap for female northern cardinals, but this finding is highly impacted by the small sample size (Table 1). For the non-color morphological traits, principal component 1 separated out individuals along an axis informed by year, bill width, tail length, and crest for male northern cardinals (Figure S4), tail length, bill width, crest, wing, and bill length for female northern cardinals (Figure S5), tail length, bill width, crest, and wing for male pyrrhuloxia (Figure S6), and tail length, wing length, and crest for female pyrrhuloxia (Figure S7). Urban and urban-outskirt birds demonstrated more variation than rural birds in northern cardinals of both sexes, but the urban categories were more similar in both sexes of pyrrhuloxia.

For all color analyses, we ran linear models with the color trait as the dependent variable and urban category, tarsus length, year, and the interaction between year and urban category as fixed effects using the lm function from the R package “stats.” We assessed multicollinearity using variance inflation factors (VIF) on each sex of each species using 3 as a cutoff, and as a result dropped both year and the interaction between urban category and year from analyses of northern cardinal females. No predictors exhibited collinearity for color analyses of northern cardinal males, pyrrhuloxia males, or pyrrhuloxia females. We assessed significance with an ANOVA on the fixed effects of the model using parametric bootstrapping with the Satterthwaite approximation for degrees of freedom applied to a restricted maximum likelihood (REML) fitted model (Luke 2017). We tested for differences in means following the ANOVA with a Tukey post-hoc test.

For all morphological analyses, we ran linear models with the morphological trait as the independent variable and urban category, tarsus length, year, and the interaction between year and urban category as fixed effects using the lm function from the R package “stats.” Tarsus was included as a fixed effect in order to account for overall body size in the model. Significance was assessed using t-statistics output from the lm model. We again assessed multicollinearity using VIFs, and as a result dropped both year and the interaction between urban category and year from analyses of northern cardinal females. No predictors exhibited collinearity for color analyses of northern cardinal males, pyrrhuloxia males, or pyrrhuloxia females.

Results

Color traits

Northern Cardinal Males

Birds from different urbanization categories differed significantly in bill hue (F_2 = 17.705, p < 0.001) and breast brightness (F_2 = 4.056, p = 0.027) (Figure 2, Table S15). Male cardinals had redder bills in urban areas compared to urban-outskirt (df = 31, p=0.014, CI = [-9.66, -0.967]) and rural areas (df = 31, p<0.001, CI = [-9.514, -2.68]). Urban birds had darker breast plumage than rural birds (df = 31, p=0.024, CI = [11.59, 0.721]).

Year had a significant effect on bill hue (F_1 = 120.152, p < 0.001), bill saturation (F_s = 9.565, p = 0.004), bill brightness (F_1 = 4.701, p = 0.038), crest brightness (F_1 = 6.382, p = 0.017), and face-mask brightness (F_1 = 13.391, p = 0.001), with older specimens having less red, less saturated, and brighter bills, as well as darker crests and brighter face masks (Table S15).

The interaction between year and urbanization category had a significant effect on face-mask saturation (F_2 = 8.040, p = 0.002), with more recent rural birds exhibiting a higher saturation than older rural birds, but more recent urban birds exhibiting a lower saturation than older urban birds, and no change over time for the urban outskirt birds (Figure S8, Table S15).

Northern Cardinal Females

We found no significant effect of urbanization category on the evaluated color traits for northern cardinal females (Table S16).

Pyrrhuloxia Males

Urbanization category had a significant effect on crest brightness (F_2 = 5.220, p = 0.013) (Figure 2, Table S17). Crests of male pyrrhuloxia were darker than those of rural birds (df = 24, p = 0.022, CI = [-14.461, -1.03]). Year had a significant effect on bill saturation (F_1 = 10.576, p = 0.003), breast hue (F_1 = 4.498, p = 0.043), and breast brightness (F_1 = 6.364, p = 0.018), with older specimens having less saturated bills, and less red, brighter breasts.

Pyrrhuloxia Females

Urbanization category had a significant effect on breast saturation of female pyrrhuloxia (F_1 = 4.448, p = 0.050), with rural birds being more saturated than urban and urban-outskirt birds (df = 17, p=0.012, CI = [2.28, 16.2]) (Figure 2, Table S18). Year had a significant effect on face brightness (F_1 = 4.802, p = 0.043), breast hue (F_1 = 15.643, p = 0.001), and breast brightness (F_1 = 10.674, p = 0.005), with older specimens having brighter faces and brighter and less red breasts.

Size traits

For male northern cardinals, we found a significant effect of urbanization category on bill width (F_2 = 3.307, p = 0.049) and tail length (F_2 = 13.440, p = <0.001) (Figure 3, Table S19). Urban birds have a wider bill than rural birds (p = 0.054) and a longer tail than both urban-outskirt and rural birds (p < 0.001 and p = 0.016 respectively). Year had a significant effect on bill length (F_2 = 6.147, p = 0.019), bill width (F_1 = 7.956, p = 0.008), and tail length (F_1 = 21.974, p = <0.001); over time, bills have gotten longer (β = -0.017) and wider (β = - 0.011), and tails have gotten longer (β = -0.139).

As with plumage, we found no effect of urbanization category on morphological traits of female northern cardinals (Table S20).

For male pyrrhuloxia, urbanization category had a significant effect on bill width (F_2 = 3.376, p = 0.049), with urban birds having a wider bill than urban-outskirt (p = 0.036, Figure 3, Table S21). Year had a significant effect on bill width (F_1 = 8.949, p = 0.006), head length, and tail length (F_1 = 9.238, p = 0.005); over time, bills have gotten wider (β = -0.011), heads have gotten longer (β = -0.034), and tails have gotten longer (β = -0.068).

For female pyrrhuloxia, there were no effects of urbanization on morphological traits (Table S22), but year had a significant effect on wing length (F_1 = 5.481, p = 0.032), with older specimens having longer wings (β = 0.024) Figure 3, Table S22).

Discussion

We found that a higher degree of habitat urbanization was associated with redder bill coloration and darker breast plumage in male northern cardinals, with darker crest plumage in male pyrrhuloxia, and less saturated breast plumage in female pyrrhuloxia. We also found that bill width increased in males of both species over time in urban and urban-outskirt regions, and that tail length increased over time for males of both species, but specifically in urban regions for male northern cardinals. Bill length increased over time for male northern cardinals, and wing length decreased over time for female pyrrhuloxia. We observed that for plumage and size traits, urbanization was not always associated with changes in the same traits between the species, but the effect of urbanization was in a consistent direction for all similar traits. However, while urbanization was consistently associated with reduced expression of carotenoids in plumage, it was associated with increased expression of carotenoids in bill color in male northern cardinals. For feather traits relevant to flight, urbanization and time were both associated with increased maneuverability. And for bill morphology, urbanization and time were both associated with larger bills.

In carotenoid-pigmented regions of both cardinal species, urbanization is associated with darker plumage. Darker plumage can be associated with greater carotenoid deposition in the bills of some birds, but no association between carotenoid content and plumage brightness has been documented (Butler et al. 2011), and further investigations into the mechanisms underlying this phenomenon are needed. The finding that male northern cardinal breasts are darker in the city of Tucson than in surrounding areas aligns with findings from Toledo, Ohio (Jones et al. 2010), but not with studies from Syracuse, New York (Baldassarre et al. 2022), which found no association between breast brightness and urbanization but an inconsistent association between urbanization and breast hue across years. We also found that male pyrrhuloxia crests were darker in the city, indicating that urban environments have similar effects on different carotenoid-pigmented plumage regions in males of the two species. However, urban male northern cardinals had redder bills than rural parts. Though unusual, this was in line with findings from Syracuse, which is the only other urban study to evaluate bill coloration in cardinals. Bill and breast coloration of both sexes of northern cardinals are used in mate choice (Jawor et al. 2003), and nothing is known about the signals involved in mate choice for pyrrhuloxia (Tweit and Thompson 2020), although it would be surprising if the red crest of pyrrhuloxia served no social function.

We also found a negative association between urbanization and melanin content in female pyrrhuloxia breast plumage. Melanin content should be correlated with hue, brightness, and saturation (McGraw et al. 2005), but none of the traits that we evaluated were significantly associated with urbanization for all three metrics. However, brightness is the most reliable predictor of melanin content in black and gray patches (McGraw 2006). The association between urbanization and female pyrrhuloxia breast brightness does suggest an effect of urbanization on female melanin, but not carotenoid, plumage pigmentation. Nothing is known about the role of plumage color variation in pyrrhuloxia, but breast color is associated with mate choice in female northern cardinals (Jawor et al. 2003). Breast plumage in both female northern cardinals and female pyrrhuloxia appears to be largely melanin-based. It has been suggested that melanin patches play more of a role in intrasexual communication (Badyaev and Hill 2000), but evidence from horned larks (*Eremophila alpestris*) shows a role for melanin patches in mate choice (de Zwaan et al. 2019). Other avian melanin-containing color patches are affected by urbanization, such as the black ties of male great tits (*Parus major*) (Yeh 2004, Senar et al. 2014). To our knowledge, ours is the first finding of a female-specific effect of urbanization on plumage color in birds. Given the lack of research on the role of melanin pigmentation in female avian social interactions and communication, especially in the context of human disturbance, this finding highlights a new avenue for future research.

Year of collection was associated with many color traits in our analyses, and much of this may be attributed to specimen degradation (Doucet and Hill 2009). In instances where temporal change was observed, older birds were less red and less saturated, but with some brighter features (male northern cardinal bills and faces, male pyrrhuloxia bills and breasts, female pyrrhuloxia faces and breasts breasts) and some less bright features (male northern cardinal crests). Brightness values are negatively associated with carotenoid content of mallard beaks but are not associated with carotenoid content in house finch feathers (Butler et al. 2011), which helps to explain the bill trends. Urban birds also exhibited darker plumages in some carotenoid patches, so we demonstrate a general pattern of darker plumages over time and in urban areas for some patches in males of both species. Melanin-rich plumages can deposit heavy metals (Isaksson et al. 2018), and heavy metal pollution is more prevalent in urban areas (Chatelain et al. 2021) and in association with mining (Rösner 1998), which could explain why the female pyrrhuloxia breast plumage (which is pigmented with melanin) is more saturated both in urban areas and in more recent specimen.

The congruous effects of urbanization on bill morphology in northern cardinals and pyrrhuloxia suggest that these species experience the same selective pressures on this trait in urban environments. This could result from selection related to foraging, as birds with larger beaks are faster at shucking larger seeds (Nagy Koves Hrabar and Perrin 2002), or to heat tolerance, as larger bills allow for greater heat dissipation without a corresponding increase in evaporative water loss (Greenberg et al. 2012, Danner et al. 2017, Tattersall et al. 2017). Studies of house finches in similar desert urban environments found contrasting patterns, as urban finches have longer but narrower bills (Badyaev et al. 2008, Giraudeau et al. 2014), with the selective effects of bird feeders listed as the probable factor. Both cardinal species frequent bird feeders around Tucson, often visiting the same feeders as house finches (pers. obs.). Other foraging factors could be affecting this trait, as both cardinal species consume many native seeds and, unlike house finches, commonly feed insects to their young (Halkin et al. 2021, Tweit and Thompson 2020), but we lack data on the foraging habits of these species in the Sonoran desert, especially with respect to urbanization. An insectivorous species in New Zealand had shorter and wider bills in association with long term urbanization, although the mechanisms underlying this pattern are not known (Amiot et al. 2022). The Sonoran Desert has become hotter and drier over the last century (Weiss and Overpeck 2005, Zhao et al. 2021), and urban areas are even hotter than the surrounding undeveloped areas (i.e. ‘heat island‘ effect; Brazel et al. 2007). While this trait could be a response increased heat, it is unclear why cardinals would have a greater need for heat tolerance than house finches. Multiple factors could be at play, as urbanization favors small and medium beetles over larger beetles, although the trends across all insects are undocumented (Diamond et al. 2015), and reduced access to water from larger insects could interact with urban heat stress to select for wider bills.

The increased length of male northern cardinal bills, but not of male pyrrhuloxia bills, over time could result from a similar selective pressure for larger bills on both species but a contrasting pressure on bill length in pyrrhuloxia. Bill length in pyrrhuloxia could be limited by their unique, more decurved bill shape (Tweit and Thompson 2020), with selection favoring stouter bills to allow for a stronger bite (van der Meij et al. 2008), or it could be limited by foraging niche partitioning if their bill shape allows them to access resources that are unavailable to northern cardinals or other competitors. It could also be limited by physiological mechanisms, if the genetic mechanism for longer bills is constrained by an unexpected tradeoff. Regardless of the underlying this difference, this finding demonstrates that foraging abilities could play a role in the success of these species in the urban environment.

Tail length increased in urban regions over time for male northern cardinals, and over time regardless of urban category for male pyrrhuloxia. Natural selection generally favors shorter tails in open environments, but longer tails in dense landscapes that require deft maneuverability (i.e. steering with a rudder; Thomas and Balmford 1995), such as urban environments. This may be species-specific, however, as great tits (*Parus major*) in the city have shorter tails than their rural conspecifics (Caizergues et al. 2021). An urban environment may represent a more open habitat to forest-adapted species like great tits, but a relatively more dense environment to these desert-adapted cardinals. Urban-rural comparisons of this trait in other northern cardinal populations that inhabit forested landscapes (i.e. across much of the eastern USA) will hopefully provide important context for the effects of human activity on this trait. The fact that tails of males of both species elongated over time and that wings of female pyrrhuloxia became shorter over time is also intriguing, as both traits are expected to allow for improved maneuverability (Swaddle and Lockwood 2003). There is no obvious trend of undeveloped areas of Arizona becoming more vegetatively dense in a relevant context for cardinals, though no areas are truly undisturbed and undeveloped in our study area. The increased heat and reduced water of the region due to recent climate change could be driving species to utilize more resource rich and interannually stable habitats along riparian and human-developed areas even in more rural environments.

The sex-specific effects of morphological traits may result from differences in sample sizes that we were able to obtain between males and females, particularly for bill width and tail length. However, these patterns could also indicate sex-specific responses to urbanization, especially given the unique effect of urbanization on female pyrrhuloxia wing length. While both sexes of northern cardinals participate in territory defense (DeVries et al. 2020), males exert much more effort in territory establishment, intrasexual conflicts, and song performance (Gould 1961, Lemon 1968, Wilke 1995), and will feed females. However, females dominantly nest build, feed young, and develop the egg. It is unknown how these sex-specific behaviors interact with heat stress. The response of female pyrrhuloxia wing length to urbanization could suggest that selection for increased maneuverability acts on wing length for female cardinals but tail length for male cardinals. We had a very small sample size of female northern cardinals, and it is possible that this prevented us from detecting a similar pattern for them as well.

Our findings demonstrate impacts of temporal and urban selection pressures on a pair of native species and highlight the need for comprehensive studies that evaluate multiple social signals and morphological traits in the context of natural and urban selection. We show that two congeneric species with a similar ecological niche can experience different phenotypic changes under novel selective landscapes in urban environments, but several traits also respond similarly between the species. We also identify a variety of traits that differ in the city that likely have social functions, and social selection on coloration may also be driving these differences in coloration. We also show that northern cardinal color signals are affected by urbanization in similar ways in a desert city as they are in the temperate deciduous forest cities of Ohio and New York, and we contribute novel findings of selection on bill length, bill width, and tail length that we hope will be examined in other cities and locations. Our findings fit into the broader landscape of exciting new urban ecological literature, and we look forward to new advances at the intersection of urban ecology, physiology, animal behavior, and evolutionary biology.

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Tables and Figures

Figure 1. Bill and breast photographs of (from top to bottom) a male northern cardinal, a female northern cardinal, a male pyrrhuloxia, and a female pyrrhuloxia. Left photographs are from field caught birds, right photographs are from University of Arizona museum specimens.

Figure 2. Effects of urbanization on color traits. The predicted median and interquartile range based on the linear model of each color trait are presented as box plots, and actual trait measurements of the specimen are presented as points. We only present the four traits for which urbanization was significant and year was not, which were bill hue and breast brightness for male northern cardinals, crest brightness for male pyrrhuloxia, and breast saturation for female pyrrhuloxia.

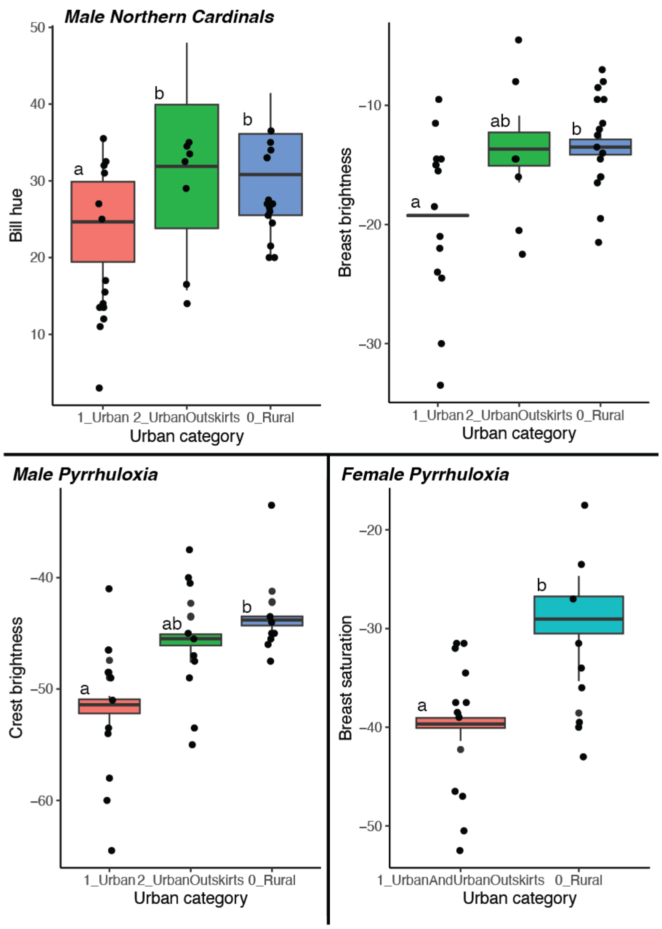


Figure 3. Effects of urbanization and time on trait sizes. The linear regressions with interquartile ranges of each trait size are presented with actual trait measurements of the specimen plotted as points. We only present the six traits for which both urbanization and year or the interaction between the two were significant, which were bill width, tail length, and bill length for male northern cardinals, bill width and tail length for male pyrrhuloxia, and wing length for female pyrrhuloxia.

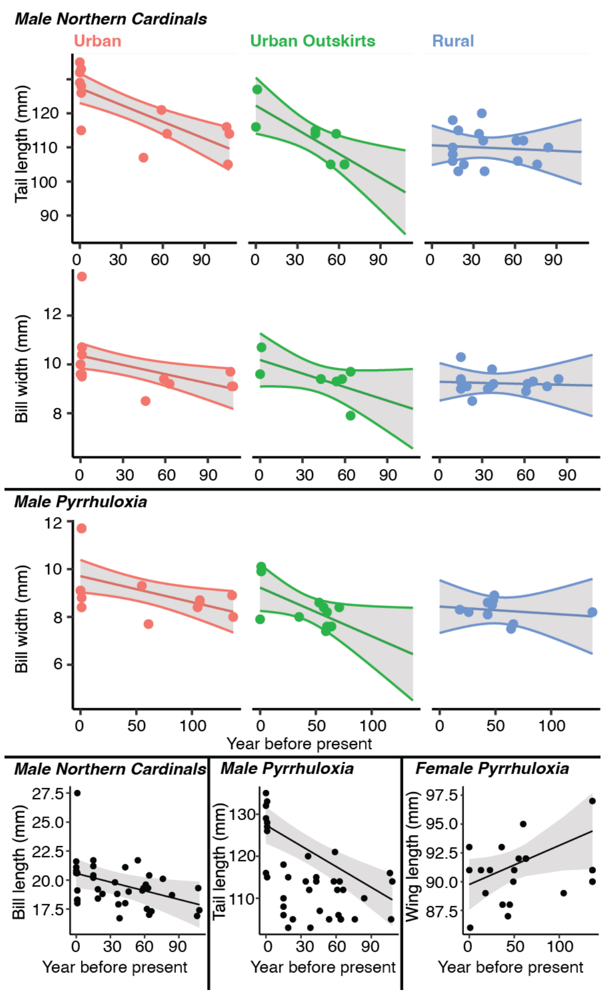


Table 1. Effects of urbanization on color traits. We only present results with either significant effects of urban category or of the interaction between urban category and year. Results of the full models can be found in the supplement (Tables S15-S18).

		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Northern Cardinal Males						
Bill						
	Hue					
	Urban_categorical	2	503.26	251.63	17.71	0.00
	Year_Adj	1	1707.63	1707.63	120.15	0.00
	Urban_categorical:Year_Adj	2	45.95	22.97	1.62	0.21
	Residuals	31	440.58	14.21		
Face						
	Saturation					
	Urban_categorical	2	106.90	53.44	0.44	0.65
	Year_Adj	1	74.80	74.81	0.62	0.44
	Urban_categorical:Year_Adj	2	1940.60	970.29	8.04	0.00
	Residuals	31	3741.10	120.68		
Breast						
	Brightness					
	Urban_categorical	2	291.56	145.78	4.06	0.03
	Year_Adj	1	0.00	0.00	0.00	1.00
	Urban_categorical:Year_Adj	2	17.73	8.86	0.25	0.78
	Residuals	31	1114.24	35.94		
Pyrrhuloxia males						
Crest						
	Brightness					
	Urban_categorical	2	348.87	174.43	5.22	0.01
	Year_Adj	1	93.07	93.07	2.78	0.11
	Urban_categorical:Year_Adj	2	2.36	1.18	0.04	0.97

	Residuals	24	802.05	33.42		
Pyrrhuloxia Females						
Face						
	Hue					
	Urban_categorical	1	9.53	9.53	0.51	0.49
	Year_Adj	1	116.96	116.96	6.21	0.02
	Urban_categorical:Year_Adj	1	90.28	90.28	4.79	0.04
	Residuals	17	320.23	18.84		
Breast						
	Saturation					
	Urban_categorical	1	283.95	283.95	5.44	0.03
	Year_Adj	1	232.01	232.01	4.45	0.05
	Urban_categorical:Year_Adj	1	60.48	60.48	1.16	0.30
	Residuals	17	886.79	52.16		

Table 2. Effects of urbanization and year on trait sizes. We only present results with either significant effects of urban category, year, or of the interaction between the two. All results can be found in the supplement (Tables S19-S22).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Northern Cardinal Males					
Bill Length					
Urban_categorical	2	2.90	1.45	0.44	0.65
Tarsus	1	13.02	13.02	3.99	0.05
Year_Adj	1	20.05	20.05	6.15	0.02
Urban_categorical: Year_Adj	2	1.71	0.85	0.26	0.77
Residuals	32	104.39	3.26		
Bill Width					
Urban_categorical	2	4.03	2.02	3.31	0.05
Tarsus	1	0.30	0.30	0.49	0.49
Year_Adj	1	4.85	4.85	7.96	0.01
Urban_categorical: Year_Adj	2	1.36	0.68	1.11	0.34
Residuals	32	19.50	0.61		
Tail Length					
Urban_categorical	2	936.68	468.34	13.44	0.00
Tarsus	1	0.14	0.14	0.00	0.95
Year_Adj	1	765.76	765.76	21.97	0.00
Urban_categorical: Year_Adj	2	201.16	100.58	2.89	0.07
Residuals	30	1045.45	34.85		
Pyrrhuloxia Males					
Bill Width					
Urban_categorical	2	4.99	2.49	3.38	0.05
Tarsus	1	0.00	0.00	0.00	0.99
Year_Adj	1	6.61	6.61	8.95	0.01
Urban_categorical: Year_Adj	2	1.29	0.64	0.87	0.43
Residuals	27	19.95	0.74		

Head Length					
Urban_categorical	2	13.60	6.80	0.86	0.43
Tarsus	1	0.52	0.52	0.07	0.80
Year_Adj	1	73.11	73.11	9.24	0.01
Urban_categorical: Year_Adj	2	12.27	6.14	0.78	0.47
Residuals	27	213.70	7.92		
Tail Length					
Urban_categorical	2	94.99	47.50	1.46	0.25
Tarsus	1	12.66	12.66	0.39	0.54
Year_Adj	1	226.39	226.39	6.98	0.01
Urban_categorical: Year_Adj	2	124.82	62.41	1.92	0.17
Residuals	23	745.87	32.43		
Pyrrhuloxia Females					
Wing Length					
Urban_categorical	1	15.08	15.08	3.34	0.09
Tarsus	1	13.86	13.86	3.07	0.10
Year_Adj	1	24.75	24.75	5.48	0.03
Urban_categorical: Year_Adj	1	1.42	1.42	0.32	0.58
Residuals	17	76.76	4.52		

<u>Supplement</u>

Figure S1. Specimen sampling by species, sex, urban category, and year.
We sampled male northern cardinals from urban (N=15), urban outskirts (N=8), and rural regions (N=16), female northern cardinals from urban and urban outskirt regions (N=4) and from rural regions (N=5), male pyrrhuloxia from urban (N=13), urban outskirts (N=11), and rural regions (N=10), and female pyrrhuloxia from urban and urban outskirt regions (N=13), and from rural regions (N=9). These samples span 137 years, from 1885 to 2022, with all subgroups of sex and urban category containing sampling across many decades.

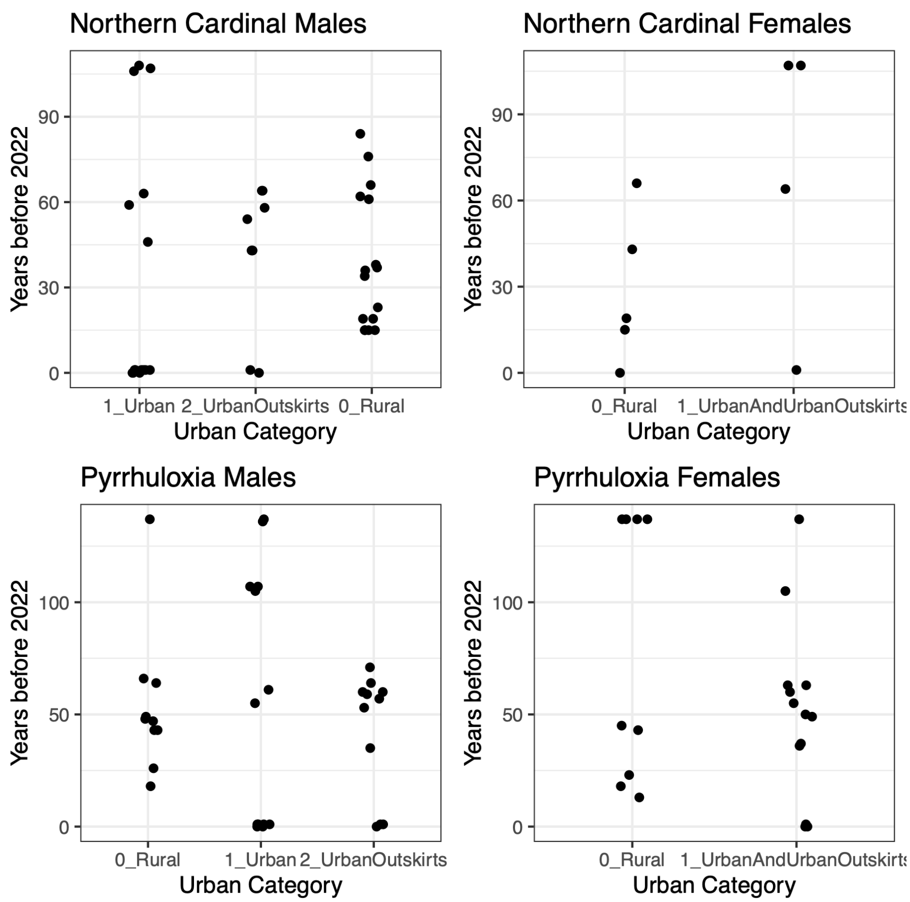


Figure S2.

Top: Histogram of urban outskirt and rural samples by distance to urban area. Blue samples are urban outskirt samples and black samples are rural samples. Urban samples were excluded from the plot as they are all at a distance of 0 from the urban area.

Bottom: *Sample locations by urban category.* Purple pins are urban, yellow/green pins are urban outskirts, dark green pins are rural

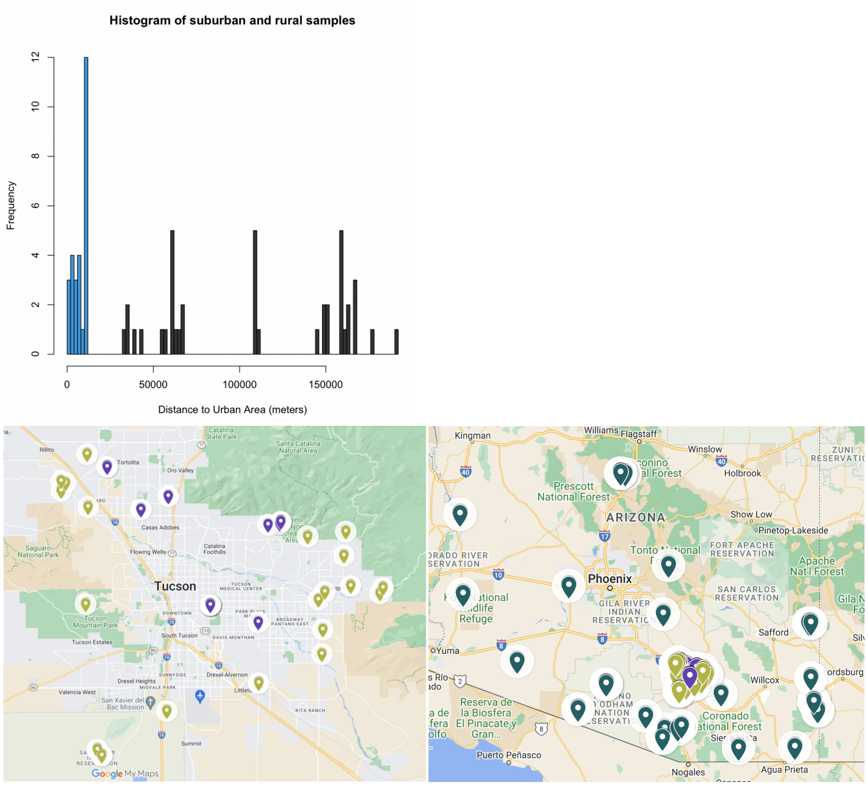
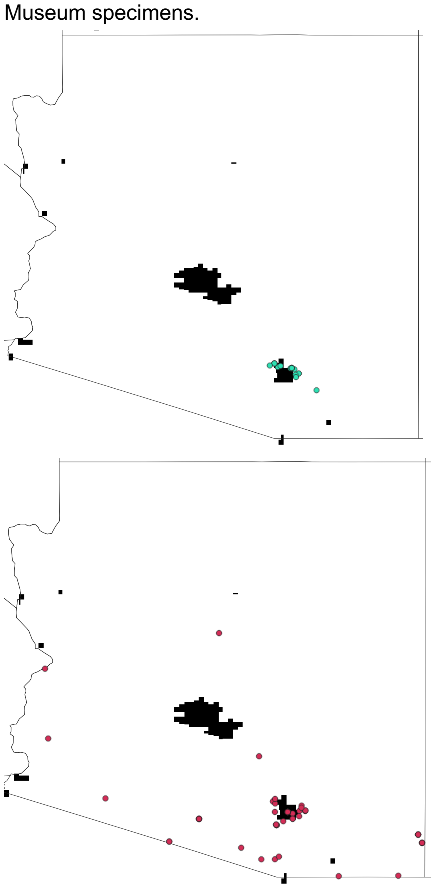


Figure S3.

Sample locations by source and model of 2020 urban areas. In each plot, the black squares represent urban areas and the points represent sampled birds. The top plot shows field samples, the middle plot shows sampling locations of the University of Arizona Museum specimens, and the bottom plot shows sampling locations of the University of Washington Burke Museum specimens.



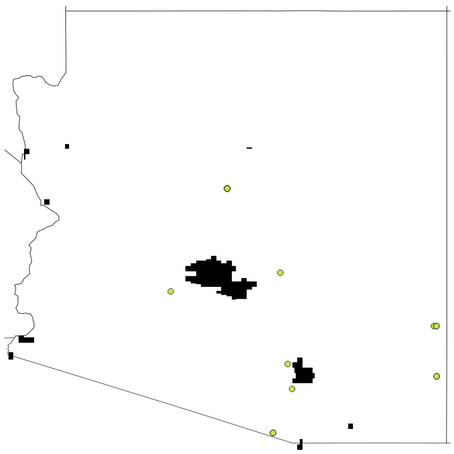


Figure S4

NOCA M PCA (Color morphology left, non-color morphology right)

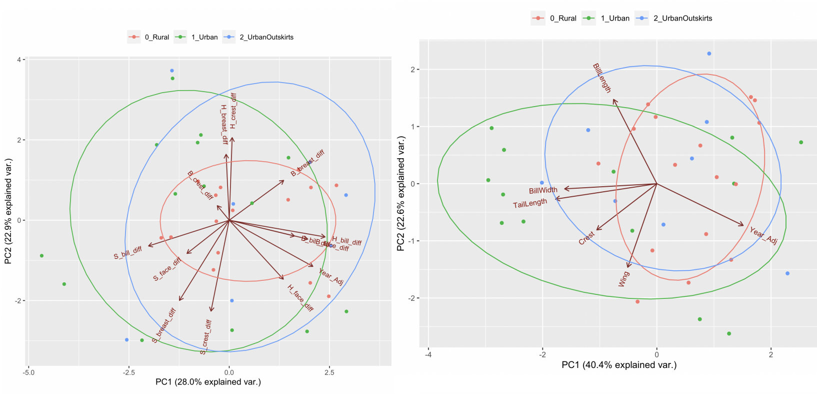


Figure S5

NOCA F PCA (Color morphology left, non-color morphology right)

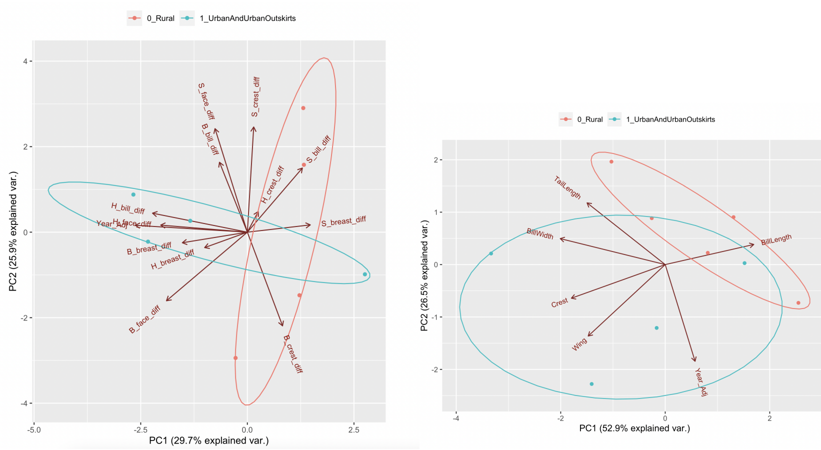


Figure S6

PYRR M PCA (Color morphology left, non-color morphology right)

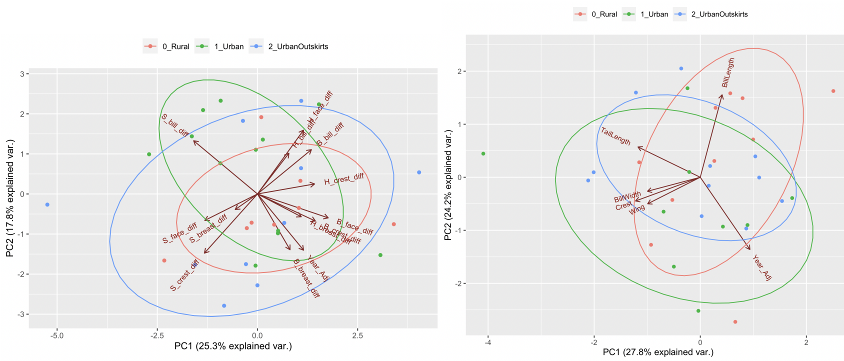


Figure S7

PYRR F PCA (Color morphology left, non-color morphology right)

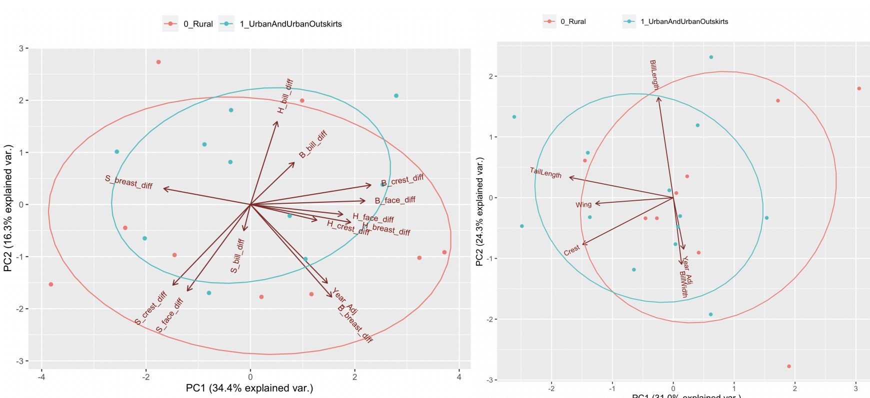


Figure S8: Interaction of year and urbanization on color traits

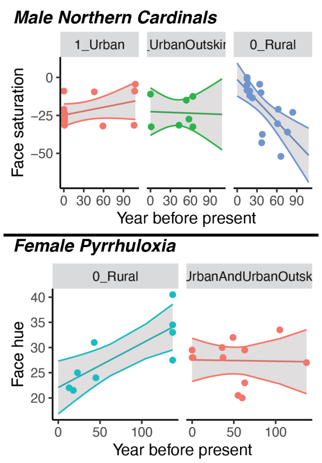


Table S1: Specimen counts

Source	**Species**	**Sex**	**Count**
Field	Northern cardinals	Female	2
		Male	11
	Pyrrhuloxia	Female	3
		Male	9
UAZ	Northern cardinals	Female	5
		Male	19
	Pyrrhuloxia	Female	17
		Male	22
UWBM	Northern cardinals	Female	2
		Male	9
	Pyrrhuloxia	Female	2
		Male	3

Correlation Tables
Table S2: NOCA M Correlation Analysis P-values

	TailLength	Crest	Wing	BillLength	BillWidth	H_bill_diff	S_bill_diff	B_bill_diff	H_crest_diff	S_crest_diff	B_crest_diff	H_face_diff	S_face_diff	B_face_diff	H_breast_diff	S_breast_diff	B_breast_diff
TailLength	NA	0.02	0.03	0.37	0.00	0.00	0.27	0.48	0.45	1.00	0.57	0.00	0.77	0.01	0.37	0.67	0.50
Crest	0.02	NA	0.20	0.87	0.01	0.19	0.91	0.33	0.23	0.58	0.95	0.04	0.25	0.70	0.04	0.84	0.51
Wing	0.03	0.20	NA	0.11	0.65	0.80	0.66	0.03	0.25	0.63	0.24	0.62	0.36	0.65	0.02	0.35	0.78
BillLength	0.37	0.87	0.11	NA	0.35	0.00	0.00	0.03	0.42	0.08	0.02	0.19	0.00	0.07	0.33	0.01	0.47
BillWidth	0.00	0.01	0.65	0.35	NA	0.00	0.10	0.84	0.60	0.86	0.66	0.00	0.15	0.11	0.09	0.66	0.12
BillHue	0.00	0.19	0.80	0.00	0.00	NA	0.00	0.00	0.12	0.90	0.28	0.00	0.19	0.00	0.94	0.13	0.06
BillSaturation	0.27	0.91	0.66	0.00	0.10	0.00	NA	0.14	0.77	0.04	0.42	0.18	0.00	0.00	0.96	0.00	0.14
BillBrightness	0.48	0.33	0.03	0.03	0.84	0.00	0.14	NA	0.02	0.46	0.98	0.28	0.00	0.00	0.46	0.96	0.38
Crest Hue	0.45	0.23	0.25	0.42	0.60	0.12	0.77	0.02	NA	0.00	0.50	0.34	0.89	0.24	0.00	0.13	0.31
Crest Saturation	1.00	0.58	0.63	0.08	0.86	0.90	0.04	0.46	0.00	NA	0.58	0.26	0.01	0.50	0.20	0.00	0.03
Crest Brightness	0.57	0.95	0.24	0.02	0.66	0.28	0.42	0.98	0.50	0.58	NA	0.45	0.27	0.48	0.62	0.39	0.00
Face Hue	0.00	0.04	0.62	0.19	0.00	0.00	0.18	0.28	0.34	0.26	0.45	NA	0.23	0.00	0.93	0.31	0.54
Face Saturation	0.77	0.25	0.36	0.00	0.15	0.19	0.00	0.00	0.89	0.01	0.27	0.23	NA	0.05	0.52	0.00	0.33
Face Brightness	0.01	0.70	0.65	0.07	0.11	0.00	0.00	0.00	0.24	0.50	0.48	0.00	0.05	NA	0.32	0.31	0.02
BreastHue	0.37	0.04	0.02	0.33	0.09	0.94	0.96	0.46	0.00	0.20	0.62	0.93	0.52	0.32	NA	0.07	0.69
BreastSaturation	0.67	0.84	0.35	0.01	0.66	0.13	0.00	0.96	0.13	0.00	0.39	0.31	0.00	0.31	0.07	NA	0.06
BreastBrightness	0.50	0.51	0.78	0.47	0.12	0.06	0.14	0.38	0.31	0.03	0.00	0.54	0.33	0.02	0.69	0.06	NA

<u>Table S3: NOCA M Correlation Analysis n-values</u>

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	37	37	37	37	37	35	35	35	34	34	34	35	35	35	35	35	35
Crest	37	37	37	37	37	35	35	35	34	34	34	35	35	35	35	35	35
Wing	37	37	39	39	39	37	37	37	36	36	36	37	37	37	37	37	37
BillLength	37	37	39	39	39	37	37	37	36	36	36	37	37	37	37	37	37
BillWidth	37	37	39	39	39	37	37	37	36	36	36	37	37	37	37	37	37
BillHue	35	35	37	37	37	37	37	37	36	36	36	37	37	37	37	37	37
BillSaturation	35	35	37	37	37	37	37	37	36	36	36	37	37	37	37	37	37
BillBrightness	35	35	37	37	37	37	37	37	36	36	36	37	37	37	37	37	37
Crest Hue	34	34	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36
Crest Saturation	34	34	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36
Crest Brightness	34	34	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36
Face Hue	35	35	37	37	37	37	37	37	36	36	36	37	37	37	37	37	37
Face Saturation	35	35	37	37	37	37	37	37	36	36	36	37	37	37	37	37	37
Face Brightness	35	35	37	37	37	37	37	37	36	36	36	37	37	37	37	37	37
BreastHue	35	35	37	37	37	37	37	37	36	36	36	37	37	37	37	37	37
BreastSaturation	35	35	37	37	37	37	37	37	36	36	36	37	37	37	37	37	37
BreastBrightness	35	35	37	37	37	37	37	37	36	36	36	37	37	37	37	37	37

Table S4: NOCA M Correlation Analysis r-values

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	1.00	0.39	0.36	0.15	0.56	-0.54	0.19	-0.12	0.13	0.00	0.10	-0.55	-0.05	-0.43	-0.16	0.07	-0.12
Crest	0.39	1.00	0.21	-0.03	0.44	-0.23	-0.02	0.17	-0.21	0.10	0.01	-0.36	-0.20	-0.07	-0.35	-0.04	-0.11
Wing	0.36	0.21	1.00	-0.26	0.07	-0.04	-0.08	0.36	-0.20	0.08	0.20	-0.08	-0.15	0.08	-0.38	0.16	0.05
BillLength	0.15	-0.03	-0.26	1.00	0.15	-0.46	0.55	-0.36	0.14	0.29	0.38	-0.22	0.49	-0.30	0.16	0.42	-0.12
BillWidth	0.56	0.44	0.07	0.15	1.00	-0.57	0.27	-0.03	0.09	-0.03	-0.08	-0.58	-0.24	-0.26	-0.28	0.07	-0.26
BillHue	-0.54	-0.23	-0.04	-0.46	-0.57	1.00	-0.54	0.46	-0.26	0.02	-0.18	0.58	-0.22	0.51	-0.01	-0.25	0.31
BillSaturation	0.19	-0.02	-0.08	0.55	0.27	-0.54	1.00	-0.24	0.05	0.34	0.14	-0.23	0.52	-0.46	0.01	0.61	-0.25
BillBrightness	-0.12	0.17	0.36	-0.36	-0.03	0.46	-0.24	1.00	-0.38	0.13	0.00	0.18	-0.46	0.47	-0.13	0.01	0.15
Crest Hue	0.13	-0.21	-0.20	0.14	0.09	-0.26	0.05	-0.38	1.00	-0.56	0.12	-0.16	-0.02	-0.20	0.52	-0.26	0.17
Crest Saturation	0.00	0.10	0.08	0.29	-0.03	0.02	0.34	0.13	-0.56	1.00	-0.10	0.19	0.40	-0.11	-0.22	0.68	-0.37
Crest Brightness	0.10	0.01	0.20	0.38	-0.08	-0.18	0.14	0.00	0.12	-0.10	1.00	-0.13	0.19	0.12	-0.08	0.15	0.48
Face Hue	-0.55	-0.36	-0.08	-0.22	-0.58	0.58	-0.23	0.18	-0.16	0.19	-0.13	1.00	0.20	0.52	0.01	0.17	0.10
Face Saturation	-0.05	-0.20	-0.15	0.49	-0.24	-0.22	0.52	-0.46	-0.02	0.40	0.19	0.20	1.00	-0.32	0.11	0.55	-0.16
Face Brightness	-0.43	-0.07	0.08	-0.30	-0.26	0.51	-0.46	0.47	-0.20	-0.11	0.12	0.52	-0.32	1.00	-0.17	-0.17	0.39
BreastHue	-0.16	-0.35	-0.38	0.16	-0.28	-0.01	0.01	-0.13	0.52	-0.22	-0.08	0.01	0.11	-0.17	1.00	-0.30	0.07
BreastSaturation	0.07	-0.04	0.16	0.42	0.07	-0.25	0.61	0.01	-0.26	0.68	0.15	0.17	0.55	-0.17	-0.30	1.00	-0.31
BreastBrightness	-0.12	-0.11	0.05	-0.12	-0.26	0.31	-0.25	0.15	0.17	-0.37	0.48	0.10	-0.16	0.39	0.07	-0.31	1.00

Table S5: NOCA F Correlation Analysis p-values

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	NA	0.13	0.93	0.09	0.00	0.15	0.95	0.44	0.73	0.19	0.42	0.22	0.08	0.95	0.39	0.73	0.75
Crest	0.13	NA	0.03	0.16	0.01	0.91	0.50	0.98	0.95	0.77	0.09	0.17	0.97	0.16	0.42	0.34	0.99
Wing	0.93	0.03	NA	0.26	0.38	0.65	0.62	0.93	0.77	0.50	0.02	0.38	0.55	0.25	0.34	0.17	0.76
BillLength	0.09	0.16	0.26	NA	0.25	0.87	0.45	0.23	0.49	0.21	0.80	0.74	0.10	0.65	0.09	0.04	0.93
BillWidth	0.00	0.01	0.38	0.25	NA	0.05	0.22	0.75	0.93	0.71	0.79	0.01	0.64	0.17	0.49	0.84	0.50
BillHue	0.15	0.91	0.65	0.87	0.05	NA	0.26	0.91	0.78	0.74	0.33	0.04	0.51	0.26	0.93	0.53	0.65
BillSaturation	0.95	0.50	0.62	0.45	0.22	0.26	NA	0.43	0.89	0.71	0.23	0.37	0.14	0.30	0.77	0.82	0.91
BillBrightness	0.44	0.98	0.93	0.23	0.75	0.91	0.43	NA	0.32	0.03	0.47	0.57	0.51	0.46	0.82	0.74	0.10
Crest Hue	0.73	0.95	0.77	0.49	0.93	0.78	0.89	0.32	NA	0.74	0.89	0.96	0.17	0.74	0.49	0.21	0.00
Crest Saturation	0.19	0.77	0.50	0.21	0.71	0.74	0.71	0.03	0.74	NA	0.29	0.46	0.18	0.14	0.76	0.91	0.76
Crest Brightness	0.42	0.09	0.02	0.80	0.79	0.33	0.23	0.47	0.89	0.29	NA	0.87	0.11	0.43	0.42	0.29	0.72
Face Hue	0.22	0.17	0.38	0.74	0.01	0.04	0.37	0.57	0.96	0.46	0.87	NA	0.71	0.02	0.67	0.87	0.67
Face Saturation	0.08	0.97	0.55	0.10	0.64	0.51	0.14	0.51	0.17	0.18	0.11	0.71	NA	0.51	0.55	0.43	0.58
Face Brightness	0.95	0.16	0.25	0.65	0.17	0.26	0.30	0.46	0.74	0.14	0.43	0.02	0.51	NA	0.49	0.57	0.69
BreastHue	0.39	0.42	0.34	0.09	0.49	0.93	0.77	0.82	0.49	0.76	0.42	0.67	0.55	0.49	NA	0.00	0.64
BreastSaturation	0.73	0.34	0.17	0.04	0.84	0.53	0.82	0.74	0.21	0.91	0.29	0.87	0.43	0.57	0.00	NA	0.27
BreastBrightness	0.75	0.99	0.76	0.93	0.50	0.65	0.91	0.10	0.00	0.76	0.72	0.67	0.58	0.69	0.64	0.27	NA

Table S6: NOCA F Correlation Analysis n-values

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8
Crest	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8
Wing	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8
BillLength	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8
BillWidth	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8
BillHue	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
BillSaturation	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
BillBrightness	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Crest Hue	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Crest Saturation	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Crest Brightness	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Face Hue	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Face Saturation	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Face Brightness	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
BreastHue	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
BreastSaturation	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
BreastBrightness	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8

Table S7: NOCA F Correlation Analysis r-values

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	1.00	0.54	-0.03	-0.60	0.85	-0.56	0.02	-0.32	-0.15	-0.51	0.33	-0.49	-0.65	-0.02	0.36	-0.15	-0.13
Crest	0.54	1.00	0.72	-0.51	0.78	-0.05	0.28	-0.01	-0.02	0.12	-0.64	-0.54	0.02	-0.55	0.33	-0.39	-0.01
Wing	-0.03	0.72	1.00	-0.42	0.33	0.19	0.21	-0.04	0.12	0.28	-0.79	-0.36	0.25	-0.46	0.39	-0.53	-0.13
BillLength	-0.60	-0.51	-0.42	1.00	-0.43	-0.07	0.31	0.48	0.29	0.50	0.11	0.14	0.62	-0.19	-0.63	0.74	-0.04
BillWidth	0.85	0.78	0.33	-0.43	1.00	-0.70	0.49	-0.14	0.04	-0.16	-0.11	-0.81	-0.20	-0.54	0.29	-0.09	-0.28
BillHue	-0.56	-0.05	0.19	-0.07	-0.70	1.00	-0.46	-0.05	0.12	0.14	-0.40	0.74	0.28	0.45	0.04	-0.26	0.19
BillSaturation	0.02	0.28	0.21	0.31	0.49	-0.46	1.00	0.32	0.06	0.16	-0.48	-0.37	0.57	-0.42	0.13	0.10	-0.05
BillBrightness	-0.32	-0.01	-0.04	0.48	-0.14	-0.05	0.32	1.00	-0.40	0.76	-0.30	-0.24	0.28	-0.31	0.10	-0.14	0.62
Crest Hue	-0.15	-0.02	0.12	0.29	0.04	0.12	0.06	-0.40	1.00	0.14	-0.06	0.02	0.54	-0.14	-0.29	0.50	-0.90
Crest Saturation	-0.51	0.12	0.28	0.50	-0.16	0.14	0.16	0.76	0.14	1.00	-0.43	-0.31	0.53	-0.57	-0.13	0.05	0.13
Crest Brightness	0.33	-0.64	-0.79	0.11	-0.11	-0.40	-0.48	-0.30	-0.06	-0.43	1.00	0.07	-0.61	0.32	-0.33	0.43	-0.15
Face Hue	-0.49	-0.54	-0.36	0.14	-0.81	0.74	-0.37	-0.24	0.02	-0.31	0.07	1.00	0.16	0.79	-0.18	0.07	0.18
Face Saturation	-0.65	0.02	0.25	0.62	-0.20	0.28	0.57	0.28	0.54	0.53	-0.61	0.16	1.00	-0.28	-0.25	0.32	-0.23
Face Brightness	-0.02	-0.55	-0.46	-0.19	-0.54	0.45	-0.42	-0.31	-0.14	-0.57	0.32	0.79	-0.28	1.00	0.29	-0.24	0.17
BreastHue	0.36	0.33	0.39	-0.63	0.29	0.04	0.13	0.10	-0.29	-0.13	-0.33	-0.18	-0.25	0.29	1.00	-0.89	0.20
BreastSaturation	-0.15	-0.39	-0.53	0.74	-0.09	-0.26	0.10	-0.14	0.50	0.05	0.43	0.07	0.32	-0.24	-0.89	1.00	-0.44
BreastBrightness	-0.13	-0.01	-0.13	-0.04	-0.28	0.19	-0.05	0.62	-0.90	0.13	-0.15	0.18	-0.23	0.17	0.20	-0.44	1.00

Table S8: PYRR M Correlation Analysis p-values

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	NA	0.72	0.92	0.83	0.70	0.26	0.55	0.97	0.03	0.52	0.52	0.93	0.77	0.29	0.14	0.26	0.20
Crest	0.72	NA	0.51	0.24	0.54	0.18	0.23	0.16	0.61	0.43	0.23	0.38	0.03	0.46	0.12	0.20	0.52
Wing	0.92	0.51	NA	0.33	0.69	0.08	0.58	0.01	0.71	0.97	0.93	0.77	0.74	0.21	0.33	0.58	0.40
BillLength	0.83	0.24	0.33	NA	0.12	0.72	0.69	0.79	0.08	0.89	0.24	0.36	0.19	0.14	0.73	0.02	0.96
BillWidth	0.70	0.54	0.69	0.12	NA	0.07	0.00	0.70	0.52	0.14	0.09	0.47	0.07	0.78	0.15	0.06	0.17
BillHue	0.26	0.18	0.08	0.72	0.07	NA	0.89	0.00	0.72	0.07	0.06	0.11	0.97	0.82	0.16	0.45	0.93
BillSaturation	0.55	0.23	0.58	0.69	0.00	0.89	NA	0.61	0.31	0.95	0.02	0.17	0.26	0.02	0.25	0.66	0.03
BillBrightness	0.97	0.16	0.01	0.79	0.70	0.00	0.61	NA	0.11	0.05	0.23	0.10	0.46	0.06	0.09	0.87	0.99
Crest Hue	0.03	0.61	0.71	0.08	0.52	0.72	0.31	0.11	NA	0.39	0.17	0.00	0.25	0.51	0.01	0.38	0.80
Crest Saturation	0.52	0.43	0.97	0.89	0.14	0.07	0.95	0.05	0.39	NA	0.37	0.01	0.04	0.38	0.63	0.05	0.80
Crest Brightness	0.52	0.23	0.93	0.24	0.09	0.06	0.02	0.23	0.17	0.37	NA	0.57	0.89	0.03	0.58	0.69	0.11
Face Hue	0.93	0.38	0.77	0.36	0.47	0.11	0.17	0.10	0.00	0.01	0.57	NA	0.03	0.80	0.16	0.21	0.76
Face Saturation	0.77	0.03	0.74	0.19	0.07	0.97	0.26	0.46	0.25	0.04	0.89	0.03	NA	0.08	0.68	0.04	0.84
Face Brightness	0.29	0.46	0.21	0.14	0.78	0.82	0.02	0.06	0.51	0.38	0.03	0.80	0.08	NA	0.75	0.40	0.20
BreastHue	0.14	0.12	0.33	0.73	0.15	0.16	0.25	0.09	0.01	0.63	0.58	0.16	0.68	0.75	NA	0.82	0.21
BreastSaturation	0.26	0.20	0.58	0.02	0.06	0.45	0.66	0.87	0.38	0.05	0.69	0.21	0.04	0.40	0.82	NA	0.15
BreastBrightness	0.20	0.52	0.40	0.96	0.17	0.93	0.03	0.99	0.80	0.80	0.11	0.76	0.84	0.20	0.21	0.15	NA

Table S9: PYRR M Correlation Analysis n-values

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	30	30	30	30	30	29	29	29	26	26	26	29	29	29	29	29	29
Crest	30	32	32	32	32	31	31	31	28	28	28	31	31	31	31	31	31
Wing	30	32	34	34	34	33	33	33	30	30	30	33	33	33	33	33	33
BillLength	30	32	34	34	34	33	33	33	30	30	30	33	33	33	33	33	33
BillWidth	30	32	34	34	34	33	33	33	30	30	30	33	33	33	33	33	33
BillHue	29	31	33	33	33	33	33	33	30	30	30	33	33	33	33	33	33
BillSaturation	29	31	33	33	33	33	33	33	30	30	30	33	33	33	33	33	33
BillBrightness	29	31	33	33	33	33	33	33	30	30	30	33	33	33	33	33	33
Crest Hue	26	28	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30
Crest Saturation	26	28	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30
Crest Brightness	26	28	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30
Face Hue	29	31	33	33	33	33	33	33	30	30	30	33	33	33	33	33	33
Face Saturation	29	31	33	33	33	33	33	33	30	30	30	33	33	33	33	33	33
Face Brightness	29	31	33	33	33	33	33	33	30	30	30	33	33	33	33	33	33
BreastHue	29	31	33	33	33	33	33	33	30	30	30	33	33	33	33	33	33
BreastSaturation	29	31	33	33	33	33	33	33	30	30	30	33	33	33	33	33	33
BreastBrightness	29	31	33	33	33	33	33	33	30	30	30	33	33	33	33	33	33

<u>Table S10: PYRR M Correlation Analysis r-values</u>

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	1.00	0.07	0.02	-0.04	0.07	0.22	0.12	-0.01	-0.43	-0.13	-0.13	0.02	0.06	-0.21	-0.28	-0.22	-0.24
Crest	0.07	1.00	0.12	-0.21	0.11	0.25	0.22	0.26	-0.10	-0.16	-0.23	0.16	-0.40	-0.14	-0.29	-0.24	-0.12
Wing	0.02	0.12	1.00	-0.17	-0.07	0.31	-0.10	0.44	0.07	-0.01	-0.02	0.05	0.06	0.22	-0.17	0.10	0.15
BillLength	-0.04	-0.21	-0.17	1.00	-0.27	0.07	0.07	-0.05	0.32	0.03	0.22	0.17	0.24	-0.26	0.06	0.39	0.01
BillWidth	0.07	0.11	-0.07	-0.27	1.00	-0.32	0.50	-0.07	-0.12	-0.28	-0.32	0.13	-0.32	0.05	-0.26	-0.34	-0.24
BillHue	0.22	0.25	0.31	0.07	-0.32	1.00	-0.03	0.66	0.07	-0.33	0.35	0.29	0.01	0.04	-0.25	0.14	-0.02
BillSaturation	0.12	0.22	-0.10	0.07	0.50	-0.03	1.00	-0.09	-0.19	-0.01	-0.44	0.25	0.20	-0.41	-0.21	-0.08	-0.39
BillBrightness	-0.01	0.26	0.44	-0.05	-0.07	0.66	-0.09	1.00	0.30	-0.35	0.23	0.29	-0.13	0.33	-0.30	-0.03	0.00
Crest Hue	-0.43	-0.10	0.07	0.32	-0.12	0.07	-0.19	0.30	1.00	-0.16	0.26	0.53	-0.22	0.12	0.44	0.17	-0.05
Crest Saturation	-0.13	-0.16	-0.01	0.03	-0.28	-0.33	-0.01	-0.35	-0.16	1.00	-0.17	-0.50	0.38	-0.17	0.09	0.36	-0.05
Crest Brightness	-0.13	-0.23	-0.02	0.22	-0.32	0.35	-0.44	0.23	0.26	-0.17	1.00	0.11	-0.03	0.40	0.10	0.08	0.30
Face Hue	0.02	0.16	0.05	0.17	0.13	0.29	0.25	0.29	0.53	-0.50	0.11	1.00	-0.38	-0.05	0.25	-0.22	-0.06
Face Saturation	0.06	-0.40	0.06	0.24	-0.32	0.01	0.20	-0.13	-0.22	0.38	-0.03	-0.38	1.00	-0.31	0.07	0.36	0.04
Face Brightness	-0.21	-0.14	0.22	-0.26	0.05	0.04	-0.41	0.33	0.12	-0.17	0.40	-0.05	-0.31	1.00	-0.06	-0.15	0.23
BreastHue	-0.28	-0.29	-0.17	0.06	-0.26	-0.25	-0.21	-0.30	0.44	0.09	0.10	0.25	0.07	-0.06	1.00	-0.04	0.22
BreastSaturation	-0.22	-0.24	0.10	0.39	-0.34	0.14	-0.08	-0.03	0.17	0.36	0.08	-0.22	0.36	-0.15	-0.04	1.00	-0.25
BreastBrightness	-0.24	-0.12	0.15	0.01	-0.24	-0.02	-0.39	0.00	-0.05	-0.05	0.30	-0.06	0.04	0.23	0.22	-0.25	1.00

<u>Table S11: PYRR F Correlation Analysis p-values</u>

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	NA	0.01	0.08	0.25	0.53	0.17	0.44	0.07	0.57	0.42	0.02	0.74	0.90	0.22	0.82	0.79	0.87
Crest	0.01	NA	0.25	0.93	0.53	0.66	0.03	0.12	0.01	0.31	0.01	0.34	0.57	0.22	0.62	0.45	0.85
Wing	0.08	0.25	NA	0.90	0.67	0.77	0.35	0.44	0.19	0.84	0.51	0.32	0.28	0.42	0.72	1.00	0.80
BillLength	0.25	0.93	0.90	NA	0.17	0.81	0.91	0.55	0.12	0.62	0.47	0.94	0.16	0.52	0.16	0.63	0.78
BillWidth	0.53	0.53	0.67	0.17	NA	0.64	0.52	0.60	0.12	0.94	0.59	0.97	0.61	0.40	0.73	0.49	0.22
BillHue	0.17	0.66	0.77	0.81	0.64	NA	0.45	0.01	0.69	0.33	0.15	0.18	0.15	0.20	0.30	0.09	0.71
BillSaturation	0.44	0.03	0.35	0.91	0.52	0.45	NA	0.75	0.50	0.46	0.53	0.37	0.78	0.49	0.41	0.30	0.27
BillBrightness	0.07	0.12	0.44	0.55	0.60	0.01	0.75	NA	0.50	0.58	0.05	0.85	0.75	0.07	0.88	0.86	0.49
Crest Hue	0.57	0.01	0.19	0.12	0.12	0.69	0.50	0.50	NA	0.80	0.09	0.54	0.86	0.21	0.19	0.16	0.01
Crest Saturation	0.42	0.31	0.84	0.62	0.94	0.33	0.46	0.58	0.80	NA	0.01	0.13	0.03	0.17	0.10	0.10	0.37
Crest Brightness	0.02	0.01	0.51	0.47	0.59	0.15	0.53	0.05	0.09	0.01	NA	0.04	0.05	0.00	0.01	0.04	0.09
Face Hue	0.74	0.34	0.32	0.94	0.97	0.18	0.37	0.85	0.54	0.13	0.04	NA	0.03	0.00	0.07	0.06	0.50
Face Saturation	0.90	0.57	0.28	0.16	0.61	0.15	0.78	0.75	0.86	0.03	0.05	0.03	NA	0.01	0.35	0.42	0.54
Face Brightness	0.22	0.22	0.42	0.52	0.40	0.20	0.49	0.07	0.21	0.17	0.00	0.00	0.01	NA	0.02	0.05	0.06
BreastHue	0.82	0.62	0.72	0.16	0.73	0.30	0.41	0.88	0.19	0.10	0.01	0.07	0.35	0.02	NA	0.00	0.00
BreastSaturation	0.79	0.45	1.00	0.63	0.49	0.09	0.30	0.86	0.16	0.10	0.04	0.06	0.42	0.05	0.00	NA	0.00
BreastBrightness	0.87	0.85	0.80	0.78	0.22	0.71	0.27	0.49	0.01	0.37	0.09	0.50	0.54	0.06	0.00	0.00	NA

Table S12: PYRR F Correlation Analysis n-values

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	22	22	22	22	22	21	21	21	19	19	19	21	21	21	21	21	21
Crest	22	22	22	22	22	21	21	21	19	19	19	21	21	21	21	21	21
Wing	22	22	22	22	22	21	21	21	19	19	19	21	21	21	21	21	21
BillLength	22	22	22	22	22	21	21	21	19	19	19	21	21	21	21	21	21
BillWidth	22	22	22	22	22	21	21	21	19	19	19	21	21	21	21	21	21
BillHue	21	21	21	21	21	21	21	21	19	19	19	21	21	21	21	21	21
BillSaturation	21	21	21	21	21	21	21	21	19	19	19	21	21	21	21	21	21
BillBrightness	21	21	21	21	21	21	21	21	19	19	19	21	21	21	21	21	21
Crest Hue	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19
Crest Saturation	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19
Crest Brightness	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19
Face Hue	21	21	21	21	21	21	21	21	19	19	19	21	21	21	21	21	21
Face Saturation	21	21	21	21	21	21	21	21	19	19	19	21	21	21	21	21	21
Face Brightness	21	21	21	21	21	21	21	21	19	19	19	21	21	21	21	21	21
BreastHue	21	21	21	21	21	21	21	21	19	19	19	21	21	21	21	21	21
BreastSaturation	21	21	21	21	21	21	21	21	19	19	19	21	21	21	21	21	21
BreastBrightness	21	21	21	21	21	21	21	21	19	19	19	21	21	21	21	21	21

Table S13: PYRR F Correlation Analysis r-values

	TailLength	Crest	Wing	BillLength	BillWidth	BillHue	BillSaturation	BillBrightness	Crest Hue	Crest Saturation	Crest Brightness	Face Hue	Face Saturation	Face Brightness	BreastHue	BreastSaturation	BreastBrightness
TailLength	1.00	0.56	0.38	0.25	-0.14	-0.31	0.18	-0.40	-0.14	0.20	-0.54	-0.08	0.03	-0.28	-0.05	0.06	0.04
Crest	0.56	1.00	0.26	-0.02	0.14	-0.10	0.47	-0.35	-0.61	0.25	-0.58	-0.22	0.13	-0.28	-0.12	0.17	-0.04
Wing	0.38	0.26	1.00	0.03	-0.10	-0.07	-0.21	0.18	-0.32	-0.05	-0.16	-0.23	0.24	-0.19	-0.08	0.00	0.06
BillLength	0.25	-0.02	0.03	1.00	-0.30	-0.06	-0.03	0.14	0.37	-0.12	0.18	0.02	-0.32	0.15	-0.32	0.11	0.07
BillWidth	-0.14	0.14	-0.10	-0.30	1.00	0.11	0.15	-0.12	-0.37	0.02	-0.13	-0.01	-0.12	-0.19	-0.08	-0.16	-0.28
BillHue	-0.31	-0.10	-0.07	-0.06	0.11	1.00	0.17	0.54	-0.10	-0.24	0.34	0.30	-0.32	0.29	0.24	-0.37	0.09
BillSaturation	0.18	0.47	-0.21	-0.03	0.15	0.17	1.00	-0.07	-0.16	0.18	-0.15	0.21	-0.07	0.16	0.19	-0.24	0.25
BillBrightness	-0.40	-0.35	0.18	0.14	-0.12	0.54	-0.07	1.00	0.17	-0.14	0.46	0.04	-0.07	0.41	-0.03	-0.04	0.16
Crest Hue	-0.14	-0.61	-0.32	0.37	-0.37	-0.10	-0.16	0.17	1.00	-0.06	0.40	0.15	-0.04	0.30	0.32	-0.34	0.55
Crest Saturation	0.20	0.25	-0.05	-0.12	0.02	-0.24	0.18	-0.14	-0.06	1.00	-0.60	-0.36	0.51	-0.33	-0.39	0.39	0.22
Crest Brightness	-0.54	-0.58	-0.16	0.18	-0.13	0.34	-0.15	0.46	0.40	-0.60	1.00	0.48	-0.45	0.73	0.55	-0.48	0.40
Face Hue	-0.08	-0.22	-0.23	0.02	-0.01	0.30	0.21	0.04	0.15	-0.36	0.48	1.00	-0.48	0.60	0.41	-0.41	0.16
Face Saturation	0.03	0.13	0.24	-0.32	-0.12	-0.32	-0.07	-0.07	-0.04	0.51	-0.45	-0.48	1.00	-0.59	-0.22	0.18	0.14
Face Brightness	-0.28	-0.28	-0.19	0.15	-0.19	0.29	0.16	0.41	0.30	-0.33	0.73	0.60	-0.59	1.00	0.50	-0.44	0.42
BreastHue	-0.05	-0.12	-0.08	-0.32	-0.08	0.24	0.19	-0.03	0.32	-0.39	0.55	0.41	-0.22	0.50	1.00	-0.75	0.63
BreastSaturation	0.06	0.17	0.00	0.11	-0.16	-0.37	-0.24	-0.04	-0.34	0.39	-0.48	-0.41	0.18	-0.44	-0.75	1.00	-0.60
BreastBrightness	0.04	-0.04	0.06	0.07	-0.28	0.09	0.25	0.16	0.55	0.22	0.40	0.16	0.14	0.42	0.63	-0.60	1.00

Table S14: Repeatability of photograph measurements (ICC3)

			H	S	B
Northern cardinals	Male	Bill	0.99	0.88	0.91
		Crest	0.98	0.91	0.89
		Face	0.90	0.92	0.86
		Breast	0.97	0.97	0.80
	Female	Bill	1.00	0.94	0.84
		Crest	0.93	0.86	0.98
		Face	0.84	1.00	0.93
		Breast	0.99	0.99	0.98
Pyrrhuloxia	Male	Bill	0.92	0.94	0.96
		Crest	0.90	0.86	0.83
		Face	0.95	0.89	0.95
		Breast	0.79	0.95	0.80
	Female	Bill	0.90	0.97	0.95
		Crest	0.88	0.95	0.79
		Face	0.80	0.94	0.83
		Breast	0.96	0.99	0.95
Both	Average		0.92	0.93	0.89
	Total average		0.91		

Table S15: Northern Cardinal Male Coloration Traits ANOVA Table

		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Bill						
	Hue					
	Urban_categorical	2	503.26	251.63	17.71	0.00
	Year_Adj	1	1707.63	1707.63	120.15	0.00
	Urban_categorical:Year_Adj	2	45.95	22.97	1.62	0.21
	Residuals	31	440.58	14.21		
	Saturation					
	Urban_categorical	2	137.18	68.59	1.00	0.38
	Year_Adj	1	656.47	656.47	9.57	0.00
	Urban_categorical:Year_Adj	2	231.98	115.99	1.69	0.20
	Residuals	31	2127.60	68.63		
	Brightness					
	Urban_categorical	2	95.63	47.81	0.60	0.55
	Year_Adj	1	372.69	372.69	4.70	0.04
	Urban_categorical:Year_Adj	2	127.32	63.66	0.80	0.46
	Residuals	31	2457.62	79.28		
Crest						
	Hue					
	Urban_categorical	2	42.97	21.48	0.60	0.55
	Year_Adj	1	27.73	27.73	0.78	0.39
	Urban_categorical:Year_Adj	2	44.17	22.08	0.62	0.55
	Residuals	30	1070.82	35.69		
	Saturation					
	Urban_categorical	2	93.83	46.92	0.64	0.54
	Year_Adj	1	164.04	164.04	2.23	0.15
	Urban_categorical:Year_Adj	2	27.64	13.82	0.19	0.83

	Residuals	30	2204.30	73.48		
	Brightness					
	Urban_categorical	2	226.02	113.01	2.32	0.12
	Year_Adj	1	310.84	310.84	6.38	0.02
	Urban_categorical:Year_Adj	2	27.34	13.67	0.28	0.76
	Residuals	30	1461.22	48.71		
Face						
	Hue					
	Urban_categorical	2	2049.20	1024.61	7.31	0.00
	Year_Adj	1	2297.50	2297.52	16.38	0.00
	Urban_categorical:Year_Adj	2	317.50	158.74	1.13	0.34
	Residuals	31	4347.50	140.24		
	Saturation					
	Urban_categorical	2	106.90	53.44	0.44	0.65
	Year_Adj	1	74.80	74.81	0.62	0.44
	Urban_categorical:Year_Adj	2	1940.60	970.29	8.04	0.00
	Residuals	31	3741.10	120.68		
	Brightness					
	Urban_categorical	2	188.59	94.30	1.75	0.19
	Year_Adj	1	722.53	722.53	13.39	0.00
	Urban_categorical:Year_Adj	2	35.92	17.96	0.33	0.72
	Residuals	31	1672.65	53.96		
Breast						
	Hue					
	Urban_categorical	2	11.23	5.62	0.47	0.63
	Year_Adj	1	19.58	19.58	1.65	0.21
	Urban_categorical:Year_Adj	2	28.86	14.43	1.22	0.31
	Residuals	31	367.13	11.84		

	Saturation					
	Urban_categorical	2	44.30	22.15	0.29	0.75
	Year_Adj	1	42.49	42.49	0.55	0.46
	Urban_categorical:Year_Adj	2	188.20	94.10	1.23	0.31
	Residuals	31	2377.81	76.70		
	Brightness					
	Urban_categorical	2	291.56	145.78	4.06	0.03
	Year_Adj	1	0.00	0.00	0.00	1.00
	Urban_categorical:Year_Adj	2	17.73	8.86	0.25	0.78
	Residuals	31	1114.24	35.94		

Table S16: Northern Cardinal Female Coloration Traits ANOVA Table

		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Bill						
	Hue					
	Urban_categorical	1	87.78	87.78	2.12	0.20
	Residuals	6	247.94	41.32		
	Saturation					
	Urban_categorical	1	40.50	40.50	0.88	0.38
	Residuals	6	275.50	45.92		
	Brightness					
	Urban_categorical	1	10.13	10.13	0.44	0.53
	Residuals	6	139.38	23.23		
Crest						
	Hue					
	Urban_categorical	1	50.00	50.00	1.27	0.30
	Residuals	6	236.38	39.40		
	Saturation					
	Urban_categorical	1	0.03	0.03	0.00	0.99
	Residuals	6	683.94	113.99		
	Brightness					
	Urban_categorical	1	72.00	72.00	1.88	0.22
	Residuals	6	229.38	38.23		
Face						
	Hue					
	Urban_categorical	1	0.50	0.50	0.01	0.91
	Residuals	6	220.00	36.67		
	Saturation					
	Urban_categorical	1	4.50	4.50	0.01	0.91
	Residuals	6	1994.00	332.33		

	Brightness					
	Urban_categorical	1	66.13	66.13	0.73	0.42
	Residuals	6	540.87	90.15		
Breast						
	Hue					
	Urban_categorical	1	105.12	105.13	3.54	0.11
	Residuals	6	178.38	29.73		
	Saturation					
	Urban_categorical	1	253.12	253.13	2.92	0.14
	Residuals	6	519.75	86.63		
	Brightness					
	Urban_categorical	1	7.03	7.03	0.16	0.71
	Residuals	6	269.94	44.99		

Table S17: Pyrrhuloxia Male Coloration Traits ANOVA Table

		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Bill						
	Hue					
	Urban_categorical	2	16.38	8.19	0.68	0.51
	Year_Adj	1	1.91	1.91	0.16	0.69
	Urban_categorical:Year_Adj	2	52.12	26.06	2.17	0.13
	Residuals	27	323.84	11.99		
	Saturation					
	Urban_categorical	2	556.60	278.32	1.76	0.19
	Year_Adj	1	1668.00	1668.05	10.58	0.00
	Urban_categorical:Year_Adj	2	1003.50	501.74	3.18	0.06
	Residuals	27	4258.30	157.71		
	Brightness					
	Urban_categorical	2	189.00	94.50	0.67	0.52
	Year_Adj	1	5.80	5.84	0.04	0.84
	Urban_categorical:Year_Adj	2	216.30	108.17	0.77	0.47
	Residuals	27	3796.20	140.60		
Crest						
	Hue					
	Urban_categorical	2	48.13	24.07	0.49	0.62
	Year_Adj	1	31.04	31.04	0.64	0.43
	Urban_categorical:Year_Adj	2	2.49	1.25	0.03	0.97
	Residuals	24	1169.53	48.73		
	Saturation					
	Urban_categorical	2	143.76	71.88	0.62	0.54
	Year_Adj	1	83.40	83.40	0.73	0.40
	Urban_categorical:Year_Adj	2	385.19	192.60	1.67	0.21

	Residuals	24	2760.89	115.04		
	Brightness					
	Urban_categorical	2	348.87	174.43	5.22	0.01
	Year_Adj	1	93.07	93.07	2.78	0.11
	Urban_categorical:Year_Adj	2	2.36	1.18	0.04	0.97
	Residuals	24	802.05	33.42		
Face						
	Hue					
	Urban_categorical	2	21.98	10.99	0.73	0.49
	Year_Adj	1	2.41	2.41	0.16	0.69
	Urban_categorical:Year_Adj	2	11.73	5.86	0.39	0.68
	Residuals	27	404.02	14.96		
	Saturation					
	Urban_categorical	2	82.77	41.38	0.48	0.62
	Year_Adj	1	0.83	0.83	0.01	0.92
	Urban_categorical:Year_Adj	2	151.83	75.91	0.88	0.42
	Residuals	27	2319.80	85.92		
	Brightness					
	Urban_categorical	2	44.40	22.20	0.36	0.70
	Year_Adj	1	124.20	124.20	2.04	0.16
	Urban_categorical:Year_Adj	2	9.78	4.89	0.08	0.92
	Residuals	27	1644.37	60.90		
Breast						
	Hue					
	Urban_categorical	2	4.98	2.49	0.21	0.81
	Year_Adj	1	53.22	53.22	4.50	0.04
	Urban_categorical:Year_Adj	2	12.29	6.15	0.52	0.60
	Residuals	27	319.48	11.83		

	Saturation					
	Urban_categorical	2	182.00	91.00	0.76	0.48
	Year_Adj	1	1.20	1.24	0.01	0.92
	Urban_categorical:Year_Adj	2	386.00	192.98	1.60	0.22
	Residuals	27	3251.00	120.41		
	Brightness					
	Urban_categorical	2	39.57	19.79	0.58	0.57
	Year_Adj	1	218.79	218.79	6.36	0.02
	Urban_categorical:Year_Adj	2	0.50	0.25	0.01	0.99
	Residuals	27	928.20	34.38		

Table S18: Pyrrhuloxia Female Coloration Traits ANOVA Table

Commented [3]: double check that you did this properly... do the VIFs indicate that i should include year*urbanization?

		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Bill						
	Hue					
	Urban_categorical	1	0.099	0.0992	0.0073	0.9327
	Year_Adj	1	4.81	4.81	0.356	0.5586
	Urban_categorical:Year_Adj	1	1.468	1.4684	0.1087	0.7457
	Residuals	17	229.694	13.5114		
	Saturation					
	Urban_categorical	1	0.67	0.67	0.01	0.93
	Year_Adj	1	0.03	0.03	0.00	0.99
	Urban_categorical:Year_Adj	1	365.14	365.14	3.97	0.06
	Residuals	17	1563.46	91.97		
	Brightness					
	Urban_categorical	1	35.81	35.81	0.31	0.58
	Year_Adj	1	2.26	2.26	0.02	0.89
	Urban_categorical:Year_Adj	1	23.42	23.42	0.20	0.66
	Residuals	17	1958.96	115.23		
Crest						
	Hue					
	Urban_categorical	1	70.01	70.01	0.76	0.40
	Year_Adj	1	2.32	2.32	0.03	0.88
	Urban_categorical:Year_Adj	1	2.19	2.19	0.02	0.88
	Residuals	15	1374.61	91.64		
	Saturation					
	Urban_categorical	1	490.68	490.68	2.75	0.12
	Year_Adj	1	43.68	43.68	0.24	0.63
	Urban_categorical:Year_Adj	1	72.20	72.20	0.40	0.53

	Residuals	15	2679.08	178.61		
	Brightness					
	Urban_categorical	1	6.51	6.51	0.12	0.73
	Year_Adj	1	140.53	140.53	2.67	0.12
	Urban_categorical:Year_Adj	1	76.39	76.39	1.45	0.25
	Residuals	15	789.87	52.66		
Face						
	Hue					
	Urban_categorical	1	9.53	9.53	0.51	0.49
	Year_Adj	1	116.96	116.96	6.21	0.02
	Urban_categorical:Year_Adj	1	90.28	90.28	4.79	0.04
	Residuals	17	320.23	18.84		
	Saturation					
	Urban_categorical	1	245.05	245.05	1.62	0.22
	Year_Adj	1	17.94	17.94	0.12	0.73
	Urban_categorical:Year_Adj	1	108.96	108.96	0.72	0.41
	Residuals	17	2570.05	151.18		
	Brightness					
	Urban_categorical	1	0.14	0.14	0.00	0.95
	Year_Adj	1	200.12	200.12	4.80	0.04
	Urban_categorical:Year_Adj	1	5.58	5.58	0.13	0.72
	Residuals	17	708.47	41.68		
Breast						
	Hue					
	Urban_categorical	1	15.75	15.75	0.9196	0.351026
	Year_Adj	1	267.918	267.918	15.6426	0.001022
	Urban_categorical:Year_Adj	1	0.167	0.167	0.0097	0.922536
	Residuals	17	291.166	17.127		

	Saturation					
	Urban_categorical	1	283.95	283.95	5.44	0.03
	Year_Adj	1	232.01	232.01	4.45	0.05
	Urban_categorical:Year_Adj	1	60.48	60.48	1.16	0.30
	Residuals	17	886.79	52.16		
	Brightness					
	Urban_categorical	1	0.22	0.22	0.01	0.94
	Year_Adj	1	441.69	441.69	10.67	0.00
	Urban_categorical:Year_Adj	1	4.43	4.43	0.11	0.75
	Residuals	17	703.45	41.38		

Table S19: Northern Cardinal Male Trait Sizes ANOVA Table

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Bill Length					
Urban_categorical	2	2.90	1.45	0.44	0.65
Tarsus	1	13.02	13.02	3.99	0.05
Year_Adj	1	20.05	20.05	6.15	0.02
Urban_categorical: Year_Adj	2	1.71	0.85	0.26	0.77
Residuals	32	104.39	3.26		
Bill Width					
Urban_categorical	2	4.03	2.02	3.31	0.05
Tarsus	1	0.30	0.30	0.49	0.49
Year_Adj	1	4.85	4.85	7.96	0.01
Urban_categorical: Year_Adj	2	1.36	0.68	1.11	0.34
Residuals	32	19.50	0.61		
Crest Length					
Urban_categorical	2	55.46	27.73	2.59	0.09
Tarsus	1	33.22	33.22	3.10	0.09
Year_Adj	1	11.85	11.85	1.11	0.30
Urban_categorical: Year_Adj	2	39.38	19.69	1.84	0.18
Residuals	30	321.66	10.72		
Head Length					
Urban_categorical	2	15.79	7.89	1.72	0.19
Tarsus	1	5.77	5.77	1.26	0.27
Year_Adj	1	0.59	0.59	0.13	0.72
Urban_categorical: Year_Adj	2	0.40	0.20	0.04	0.96
Residuals	32	146.64	4.58		
Tail Length					
Urban_categorical	2	936.68	468.34	13.44	0.00
Tarsus	1	0.14	0.14	0.00	0.95
Year_Adj	1	765.76	765.76	21.97	0.00

Urban_categorical: Year_Adj	2	201.16	100.58	2.89	0.07
Residuals	30	1045.45	34.85		
Wing Length					
Urban_categorical	2	19.14	9.57	0.72	0.49
Tarsus	1	24.67	24.67	1.86	0.18
Year_Adj	1	1.42	1.42	0.11	0.75
Urban_categorical: Year_Adj	2	0.67	0.33	0.03	0.98
Residuals	32	423.85	13.25		

Table S20: Northern Cardinal Female Trait Sizes ANOVA Table

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Bill Length					
Urban_categorical	2	4.47	2.24	1.52	0.30
Tarsus	1	0.01	0.00	0.00	0.96
Residuals	5	7.35	1.47		
Bill Width					
Urban_categorical	2	0.32	0.16	0.45	0.66
Tarsus	1	0.06	0.06	0.17	0.69
Residuals	5	1.75	0.35		
Crest Length					
Urban_categorical	2	17.02	8.51	1.36	0.34
Tarsus	1	17.82	17.82	2.84	0.15
Residuals	5	31.38	6.28		
Head Length					
Urban_categorical	2	11.52	5.76	1.79	0.26
Tarsus	1	0.74	0.74	0.23	0.65
Residuals	5	16.06	3.21		
Tail Length					
Urban_categorical	2	8.70	4.35	0.06	0.95
Tarsus	1	1.24	1.24	0.02	0.90
Residuals	5	392.06	78.41		
Wing Length					
Urban_categorical	2	15.86	7.93	4.36	0.08
Tarsus	1	8.61	8.61	4.73	0.08
Residuals	5	9.09	1.82		

Table S21: Pyrrhuloxia Male Trait Sizes ANOVA Table

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Bill Length					
Urban_categorical	2	2.37	1.18	1.72	0.20
Tarsus	1	0.01	0.01	0.01	0.92
Year_Adj	1	1.94	1.94	2.82	0.10
Urban_categorical: Year_Adj	2	4.30	2.15	3.12	0.06
Residuals	27	18.59	0.69		
Bill Width					
Urban_categorical	2	4.99	2.49	3.38	0.05
Tarsus	1	0.00	0.00	0.00	0.99
Year_Adj	1	6.61	6.61	8.95	0.01
Urban_categorical: Year_Adj	2	1.29	0.64	0.87	0.43
Residuals	27	19.95	0.74		
Crest Length					
Urban_categorical	2	8.78	4.39	0.48	0.62
Tarsus	1	5.61	5.61	0.62	0.44
Year_Adj	1	7.88	7.87	0.87	0.36
Urban_categorical: Year_Adj	2	1.65	0.82	0.09	0.91
Residuals	25	227.59	9.10		
Head Length					
Urban_categorical	2	13.60	6.80	0.86	0.43
Tarsus	1	0.52	0.52	0.07	0.80
Year_Adj	1	73.11	73.11	9.24	0.01
Urban_categorical: Year_Adj	2	12.27	6.14	0.78	0.47
Residuals	27	213.70	7.92		
Tail Length					
Urban_categorical	2	94.99	47.50	1.46	0.25
Tarsus	1	12.66	12.66	0.39	0.54
Year_Adj	1	226.39	226.39	6.98	0.01

Urban_categorical: Year_Adj	2	124.82	62.41	1.92	0.17
Residuals	23	745.87	32.43		
Wing Length					
Urban_categorical	2	0.17	0.08	0.02	0.98
Tarsus	1	16.42	16.42	2.94	0.10
Year_Adj	1	0.78	0.78	0.14	0.71
Urban_categorical: Year_Adj	2	8.74	4.37	0.78	0.47
Residuals	27	150.96	5.59		

Table S22: Pyrrhuloxia Female Trait Sizes ANOVA Table

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Bill Length					
Urban_categorical	1	0.06	0.06	0.06	0.81
Tarsus	1	8.58	8.58	7.87	0.01
Year_Adj	1	1.13	1.13	1.04	0.32
Urban_categorical: Year_Adj	1	0.49	0.49	0.45	0.51
Residuals	17	18.52	1.09		
Bill Width					
Urban_categorical	1	0.09	0.09	0.22	0.64
Tarsus	1	0.69	0.69	1.78	0.20
Year_Adj	1	0.39	0.39	1.02	0.33
Urban_categorical: Year_Adj	1	0.22	0.22	0.56	0.46
Residuals	17	6.55	0.39		
Crest Length					
Urban_categorical	1	6.27	6.27	0.65	0.43
Tarsus	1	28.72	28.72	2.96	0.10
Year_Adj	1	0.31	0.30	0.03	0.86
Urban_categorical: Year_Adj	1	0.38	0.38	0.04	0.84
Residuals	17	164.92	9.70		
Head Length					
Urban_categorical	1	0.00	0.00	0.00	0.99
Tarsus	1	8.29	8.29	1.47	0.24
Year_Adj	1	18.59	18.59	3.30	0.09
Urban_categorical: Year_Adj	1	10.31	10.31	1.83	0.19
Residuals	17	95.74	5.63		
Tail Length					
Urban_categorical	1	123.14	123.14	2.26	0.15
Tarsus	1	23.57	23.57	0.43	0.52
Year_Adj	1	16.97	16.97	0.31	0.58

Urban_categorical: Year_Adj	1	6.14	6.14	0.11	0.74
Residuals	17	927.13	54.54		
Wing Length					
Urban_categorical	1	15.08	15.08	3.34	0.09
Tarsus	1	13.86	13.86	3.07	0.10
Year_Adj	1	24.75	24.75	5.48	0.03
Urban_categorical: Year_Adj	1	1.42	1.42	0.32	0.58
Residuals	17	76.76	4.52		