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Juvenile Ornamentation: Its Evolution, Genetic Basis, And Variation Across Habitats

Angela Tringali
University of Central Florida

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JUVENILE ORNAMENTATION: ITS EVOLUTION, GENETIC BASIS, AND VARIATION
ACROSS HABITATS

by

ANGELA TRINGALI
B.S. ~ State University of New York College of Environmental Science and Forestry, 2006

A dissertation submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Conservation Biology
in the Department of the Biological Sciences
in the College of Sciences
at the University of Central Florida
Orlando, Florida

Fall Term
2013

Major Professors: Reed Noss & Reed Bowman

ABSTRACT

Ornamental traits are considered honest advertisements of fitness, and their evolution is usually explained in terms of sexual selection. This explanation remains unsatisfactory in some instances, for example, juvenile birds whose plumage is molted prior to adulthood and breeding. I first evaluate whether juvenile plumage reflectance signals dominance status in the Federally Threatened Florida scrub-jay (*Aphelocoma coerulescens*) using a combination of observational and experimental methods. Then I estimate the heritability, non-genetic maternal and environmental effects, and strength of selection on juvenile plumage reflectance using archived feather samples and a pedigree constructed from historical nest records. Finally, I compare plumage reflectance and its use as a signal between a wildland and suburban population of scrub-jays. I conclude that plumage reflectance is a signal of dominance, and that social selection can also drive the evolution of sexually dimorphic traits. In this species, plumage reflectance is heritable and influenced by maternal effects, but environmental effects are inconsequential. Although this trait appears to have an important function, only mean brightness and female hue are associated with lifetime reproductive success. Plumage reflectance was more UV-shifted in the suburban birds, but there is no reason to believe that urbanization decreases the value of this plumage as a signal. However, these plumage differences may facilitate dispersal from suburban areas, contributing to the decline of suburban populations.

For Dr. Guy A. Baldassarre, who told me to look up and in doing so, opened my eyes to the

world of feathered things.

ACKNOWLEDGMENTS

I also owe my thanks to past and current members of the biology community at the University of Central Florida. Thanks to my labmates in the SPICE lab: Rob and Jill Aldredge, Joyce Klaus, Marianne Korosy, and later Joe Figel, Molly Grace, Courtney Knickerbocker, Pam Panozzo and Josh Reece. Thanks to Jane Waterman and Jim Roth, who let me attend their lab meetings and helped me settle into the swing of graduate school. Thanks to James Angelo, Simona Ceriani, and Stacy Knight for being the first friends I made, and some of the best friends and colleagues I'll ever have. Special thanks to Jessica Hightower, Ian Kutch, Lina Sanchez-Clavejo, Monette Schwoerer, and Matt Tye, for letting me bounce ideas off them and having complementary skill sets to my own.

Finally, I'd like to thank my family for being my most enthusiastic supporters. Thanks for encouraging me, even when it meant encouraging me to travel far from home, and for having confidence in me, even when confidence in myself was waning. Special thanks to my husband Joe, for making my long work-days and field seasons work for us. This wouldn't have been possible without all of your help.

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CHAPTER ONE ~ INTRODUCTION

Evolution of Ornamental Traits

The evolution and persistence of costly ornamental traits are paradoxical because they appear superfluous. This paradox formed the catalyst for Darwin's theory of sexual selection, that these traits are beneficial for mate acquisition. Both Fisher's runaway selection and Zahavi's handicap hypothesis explain the evolution of ornamental traits in terms of sexual selection (Krebs & Davies 1993). However, sexual selection is an unlikely mechanism for evolution of juvenile ornamentation, especially in avian species that molt juvenile plumage before sexual maturity. Ornamental traits may evolve by other selective forces and exploring these possibilities will expand understanding of trait evolution.

In order for a trait to evolve, some component of its variability must be heritable. Although avian coloration has been studied extensively, relatively little is known about its heritability (Mundy 2006). Understanding patterns of heritability, such as whether a trait is autosomal or sex-linked, and selection (via increased survival or reproduction) help us understand how these traits evolve and are maintained in populations.

Goals of This Study

My first objective is to examine whether juvenile Florida scrub-jay plumage is used as a signal of dominance. Because traits must be heritable to evolve, my second goal is to estimate the heritability of and strength of selection on plumage color. My third objective is to evaluate differences in plumage color, its relationship with condition, and its use as a signal between a

suburban and wildland site. I will address these goals using both experimental and observational methods as well as historical data.

Florida Scrub-Jays as Model Organisms

The Florida scrub-jay (*Aphelocoma coerulescens*) is an excellent model system to evaluate both explanations for the evolution of ornamental traits that do not rely on sexual selection and variability of ornamentation across habitats. Although Florida scrub-jays appear monomorphic to the human eye, both adults and juveniles are sexually dimorphic in the ultra-violet (UV) spectrum and in juveniles, this coloration is condition-dependent (Siefferman et al. 2008; Bridge et al. 2008). Juveniles molt before breeding (Bancroft & Woolfenden 1982) and juvenile plumage does not predict reproductive success (Siefferman et al. 2008), so sexual selection is an implausible explanation for their ornamentation.

Florida scrub-jays are cooperative breeders and their complex social structure allows us to consider whether juvenile coloration signals dominance. Within family-groups, Florida scrub-jays form rigid dominance hierarchies, where all males are dominant over all females, and breeders over non-breeders (Woolfenden & Fitzpatrick 1977). Dominance hierarchies also exist among same-aged siblings, and juvenile coloration may signal status.

The social structure of Florida scrub-jays also makes them interesting to study from a quantitative genetics standpoint. Florida scrub-jays are despotic cooperative breeders (Woolfenden & Fitzpatrick 1985). Breeding pairs are socially and genetically monogamous, which allows me to determine paternity from field observations (Townsend et al. 2011). A marked population of Florida scrub-jays has been studied at Archbold since 1969, which provides a deep pedigree for my analysis. Florida scrub-jays disperse short distances and males

frequently acquire territory, all or in part, from their fathers, so that both genes and environments are inherited (Woolfenden & Fitzpatrick 1985). This pattern, combined with generalized linear mixed models, allows me to partition genetic and environmental variance in plumage color.

I can make habitat comparisons between plumage reflectance, its condition-dependence and use as a signal because Florida scrub-jays live in both wildland and suburban areas. The Florida scrub-jay, a Federally Threatened species, is a habitat specialist, preferring oak-dominated scrub habitats with a low and open structure that is maintained by frequent fire. As of 1992-1993, 30% percent of all Florida scrub-jays live in suburban areas, but these populations are declining throughout the state (Bowman 1998; Breininger 1999). Suburban nestlings are lighter, grow more slowly, suffer greater rates of starvation, and higher rates of post-fledging mortality than wildland birds, suggesting that habitat-specific differences in condition exist (Bowman & Woolfenden 2001; Shawkey et al. 2004). Because of these habitat specific differences in nestling welfare, I predict differences in plumage ornamentation and its relationship with condition. Because signals may rely on a relationship with condition to ensure that they are honest advertisements of fitness, differences in the condition-dependence of plumage may result in a breakdown of plumage signaling.

Florida scrub-jays are non-migratory, defend all-purpose territories year round, and disperse relatively short distances (Woolfenden & Fitzpatrick 1985). Wildland birds rarely disperse to the suburbs, but suburban birds commonly disperse to the wildlands (Thaxton & Hingtgen 1996). Differences in use of plumage signal between habitats may have consequences for dispersal and settlement from suburban to wildland populations.

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CHAPTER TWO ~ PLUMAGE REFLECTANCE SIGNALS DOMINANCE IN FLORIDA SCRUB-JAY, *APHELOCOMA COERULESCENS*, JUVENILES[1]

Introduction

The evolution and persistence of costly ornamental traits are paradoxical because these traits appear superfluous. This paradox provided the catalyst for Darwin's theory of sexual selection. Sexual selection via both female choice and male-male competition often is implicated as a mechanism for explaining ornamentation and behaviour that is costly (Anderssen 1994). However, sexual selection is an unlikely mechanism for evolution of juvenile ornamentation, especially in avian species that molt juvenile plumage before sexual maturity. Alternatively, juvenile sexual dimorphism may result from a developmental constraint of sexual selection on adults. However, many avian species exhibit delayed plumage maturation, defined by Hawkins et. al (2012) as the "delayed acquisition of a definitive colour and pattern of plumage until after the individual's first potential breeding period". The existence of a different sub-adult plumage suggests that plumage colouration is not developmentally constrained.

Ornamental traits that depend on body condition may be honest advertisements of fitness (Kodric-Brown and Brown 1984). Ultra-violet (UV) colouration is related to body condition in some species (Hill 2006; Kemp 2008), although Peters et. al (2011) note that much of the evidence for this relationship is correlational and demonstrate that UV blue coloration is not condition-dependent in the blue tit (*Cyanistes caeruleus*). Regardless of correlations with body condition, UV colouration is a sexually selected trait in several taxa (spiders: Lim et al.

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[1] Published as Tringali, A. & Bowman, R. 2012. Plumage reflectance signals dominance in Florida scrub-jay, *Aphelocoma coerulescens*, juveniles. *Animal Behaviour*, **84**, 1517-1522.

2008; butterflies: Kemp 2008; fish: Rick & Bakker 2008; lizards: LeBas & Marshall 2000; birds: Andersson & Amundsen 1997, Alonso-Alvarez et al. 2004, Poesel et al. 2007) and UV reflectance is associated with intra-sexual competition in blue tits (*Cyanistes caeruleus*) (Alonso-Averez et al. 2004, Midamegbe et. al 2011) and Eastern bluebirds (*Sialia sialis*) (Siefferman and Hill 2005).

Although the use of UV-blue plumage in intra-sexual competition suggests it may signal general competitive ability, it has only been demonstrated to affect dominance interactions among unfamiliar yearling male blue tits (Vedder et. al 2010). Otherwise, little evidence exists to support status signaling in the absence of sexual selection for UV-blue plumage (Korsten et al. 2007, Vedder et al. 2008). In contrast to structural UV-blue plumage, the relationship between both melanin (Rohwer 1975, Moller 1987) and carotenoid (Pryke et. al 2002, Murphy et al. 2009) based colouration and status is well documented.

Florida scrub-jays appear monomorphic to the human eye, but both adults (Bridge et al. 2008) and juveniles (Siefferman et al. 2008) are sexually dimorphic in the UV spectrum. In Florida scrub-jays ninety-eight percent of males and ninety-five percent of females first breed in their second year or later (Woolfenden andFitzpatrick 1984), meaning that individuals molt at least once before breeding (Bancroft and Woolfenden 1982). Thus, sexual selection is an implausible explanation for juvenile ornamentation.

Florida scrub-jays breed cooperatively, forming groups which may include related and unrelated helpers (Woolfenden and Fitzpatrick 1984). Despite the presence of unrelated group members, genetic monogamy is maintained, with less than 1% of offspring sired by an extra-pair male (Townsend et. al 2011). Within family-groups, Florida scrub-jays form rigid dominance hierarchies, where all males are dominant over all females, and breeders over non-breeders

(Woolfenden and Fitzpatrick 1977). Dominance hierarchies also exist among same-aged siblings (Tringali, unpublished), and we hypothesize that the sexually dimorphic, condition-dependent plumage colouration of juvenile Florida scrub-jays (*Aphelocoma coerulescens*) signals dominance status.

To test our hypothesis we made behavioral observations of same-aged siblings on their natal territory before and after a plumage reflectance reduction treatment. We predicted that individuals with higher brightness, UV chroma, or hue are more likely to be dominant. However, the existence of this relationship does not demonstrate that plumage signals dominance, rather, only that they are correlated. To determine if plumage reflectance signals dominance we experimentally reduced plumage reflectance and compared the change in proportion of interactions won before and after manipulation. The status-signaling hypothesis would be refuted if, after reflectance reduction, dominance remained unchanged. If dominance changes in response to plumage manipulation, we can conclude that plumage signals status. We expected that manipulated birds would decrease in dominance because feedback between signals and aggression exists, particularly among younger birds (Vedder et. al 2010).

Methods

Study Site and Population

We studied a population of individually-marked Florida scrub-jays at Archbold Biological Station, Highlands County, Florida, USA (27$^°$10'N, 81$^°$21'W) in the summers of 2008-2011. As part of an ongoing long-term demographic study, all nests are found and nestlings banded with both a USFW metal band and a single colour band 11 days post-hatch (Woolfenden and Fitzpatrick 1984). Researchers are able to distinguish brood mates because each nestling receives

a different colour band and young remain on their natal territory after fledging. Nestlings also are weighed, measured, and a blood sample is collected for genetic sex determination. At nutritional independence (approx. 80-90 d post-hatch) individuals are caught in Potter Traps, re-measured and given a unique colour band combination, so that each individual in the population is identifiable. Additionally, a blood sample and the outermost right rectrix are collected.

Behavioral Observations

Beginning in June, when juveniles start to forage independently (~65 d post-hatch), we trained them to take peanut bits from a 15 cm tall gravity feeder placed on the ground. This feeder has a single small opening, which allows only one bird to feed at a time. We presented juveniles with the feeder daily for about 15 minutes a day, until all juveniles in a family would reliably retrieve peanut bits. Then we recorded all dyadic interactions among brood mates at the feeder using a digital camcorder mounted on a tripod. We observed groups daily until a linear hierarchy could be determined and terminated each observation when birds ceased to return to the feeder immediately after caching.

The recordings were reviewed in the lab by a single researcher (A.T.), who tallied displacements, pecks, bites, and physical fights between same-aged siblings and the identities of the individuals involved. For each interaction the initiator of the aggressive interaction was assigned the win and the recipient of the aggression the loss. After all observations of a group were completed, we calculated the proportion of interactions won for each pairwise combination of siblings. Following Drews' (1993) definition of dominance as a consistent pattern in outcomes of antagonistic interactions between individuals, with the winner being dominant and the loser subordinate, we considered one individual dominant over another if it won the majority of

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interactions within that dyad. Then we ranked siblings from most to least dominant, the most dominant individual being dominant over all siblings and the least over none.

To compare our behavioral measure of dominance with aggression, we looked at series of interactions between the same pair of individuals with no more than two seconds between each interaction. For each pair we recorded who initiated the first interaction (the aggressor) and the proportion of interactions the initiator won within that series. Then, for each unique pairwise combination of siblings, we averaged these measures across series.

Spectroscopy

We quantified reflectance of the outermost right rectrix from each juvenile that reached nutritional independence using an Ocean Optics USB-4000 spectrometer, a DH-2000 deuterium halogen light source, and a bifurcated fiber optic probe (Ocean Optics, Dunedin, FL). We held the probe at a $90^{°}$ angle 0.5 cm from the feather to obtain measurements from an illuminated circle with an area of 3.14 mm^2. We used this method to measure and average three points on each feather sample: 1, 2, and 3 cm from the distal end. We calculated mean brightness, UV chroma, and hue (Montgomerie 2006).

Plumage Manipulation Experiment

To experimentally manipulate plumage of the treated individuals we used art markers to colour all blue feathers, including the coverts, flight and tail feathers, and occasionally contour feathers on the head. To reduce reflectance we used a black Sharpie marker, which absorbs some light before it reaches the feather microstructure, uniformly reducing reflectance without changing the shape of the spectral curve (Liu et al. 2007). We used a Prismacolor Colorless

Blender marker as our sham control treatment. The sham control treatment does not change reflectance, but mimics the additional handling required for the reflectance reduction treatment. We did not manipulate the plumage of control birds.

After the dominance hierarchy among brood-mates was established, we sequentially assigned the dominant juvenile in each group to one of three treatment groups: unmanipulated control, sham control (colourless marker), or UV reduction (black marker). Individuals were assigned to treatments irrespective of sex because genetic sex results were not available at the time of data collection and juveniles are sexually monomorphic in human-visible plumage patterns. At nutritional independence (~85 d post-hatch) we captured all juveniles on a territory the same morning using Potter traps. After completing our general banding protocol, we released subordinate and unmanipulated control individuals, then manipulated plumage and released individuals in the sham control and reflectance reduction treatment groups. Beginning the morning after capture, we resumed dominance observations at the feeder daily for five days.

Statistical Analyses

We used one-tailed binomial tests to determine if males were more likely than females to be dominant and if plumage reflectance was associated with dominance. To determine if individuals with higher UV chroma were more likely to be dominant over their same aged siblings we ranked each individual within its group for dominance and UV chroma. We scored each sibling dyad where the dominant individual was also ranked first for UV chroma a "success". Then we calculated the binomial z-ratio, using a probability of 0.5 (the dominant individual is equally likely to have higher or lower UV chroma than the subordinate) using R.

We repeated this procedure for measures of brightness and hue. Then we repeated these analyses

for dyads where both individuals were of the same sex.

To distinguish between aggression and dominance, we used one-tailed binomial tests to

determine if dominants were more like to initiate a series of interactions and if they were more

likely to win more than half of the interactions within that series. To determine if subordinates

could increase their chances of winning by initiating interactions we used a paired t-test to

compare the proportion of interactions a subordinate won in series that it initiated with its overall

proportion of interactions won against that particular individual.

We performed ANOVA to determine if year differences in mean brightness, UV chroma,

hue, mass, number of juveniles per group, or body condition existed. We used the residuals from

the regression of mass on tarsus ($R^2 = 0.21$, $p < 0.001$) as an estimate of body condition. We

determined if the difference in body condition between the highest and lowest condition

juveniles varied with the number of juveniles in a group using linear regression.

To evaluate the effectiveness of the plumage reflectance reduction we compared the

mean brightness, UV chroma, and hue of a subset of 33 feathers before and after manipulation.

We calculated the difference in mean brightness, UV chroma and hue for each sample and used a

one-way ANOVA and a priori contrasts to test for significant differences.

To analyze our experimental data, we calculated the proportion of interactions the

dominant juvenile "won" before and after treatment and then calculated the difference between

these proportions (Δ proportion = $P(win_{after})$ - $P(win_{before})$). We used an ANOVA to compare Δ

proportion of interactions won among treatment groups, including year and sex in the model. For

families with more than 2 juveniles, we choose the dyad that included the dominant individual

and the individual with whom they had the most interactions. We used a priori contrasts to

determine if significant differences existed in Δ proportion of interactions won between (a) unmanipulated and sham controls and (b) the controls and the reflectance reduction treatment. We used R 2.8.1 (R Core Development Team, 2008) for all analyses.

Ethical Note

All capture, handling, marking, sampling, and observing of Florida scrub-jays was completed under permits from the United States (US) Geological Survey Bird Banding Lab (no. 07732), US Federal Fish and Wildlife Service (no. TE824723-7), and Florida Fish and Wildlife Conservation Commission (LSSC-10-00205) to RB, and followed protocols approved by the University of Central Florida Institutional Animal Care and Use Committee.

Behavioral observations were done at a feeder to increase the number of antagonistic interactions, however the intensity of aggression observed was not outside the range of behavior for scrub-jays when food is not provided. Additionally, no individuals were injured while using the feeder. Observations were done on free-living birds, which were not dependent on food from the feeder, allowing subordinate birds to avoid the feeder. Finally, the plumage manipulations did not impede flight, and all markers used were non-toxic.

Results

While testing our first prediction, we observed 76 juveniles in 33 groups divided into 59 same-aged sibling dyads. Males were more likely than females to be dominant ($p = 0.05$) and to have higher UV chroma ($p = 0.02$). Dominant individuals were not more likely to have higher mean brightness, UV chroma, or hue than would be expected by chance. Although no significant annual variation existed in the differences in colour, condition, or size between siblings, the

mean number of juveniles per group differed by year ($F_{1,\,61} = 9.932$, $p = 0.0025$) and the difference in body condition among siblings varied with the number of siblings in each group ($R^2 = 0.14$, $p = 0.002$), so that larger broods showed greater differences in condition.

Dominant individuals were both more likely to initiate a series of interactions (p = 0.03) and to win them (p = 0.001). However, when subordinates initiated a series of interactions, they were more likely to win that series (t = 3.72, p = 0.002).
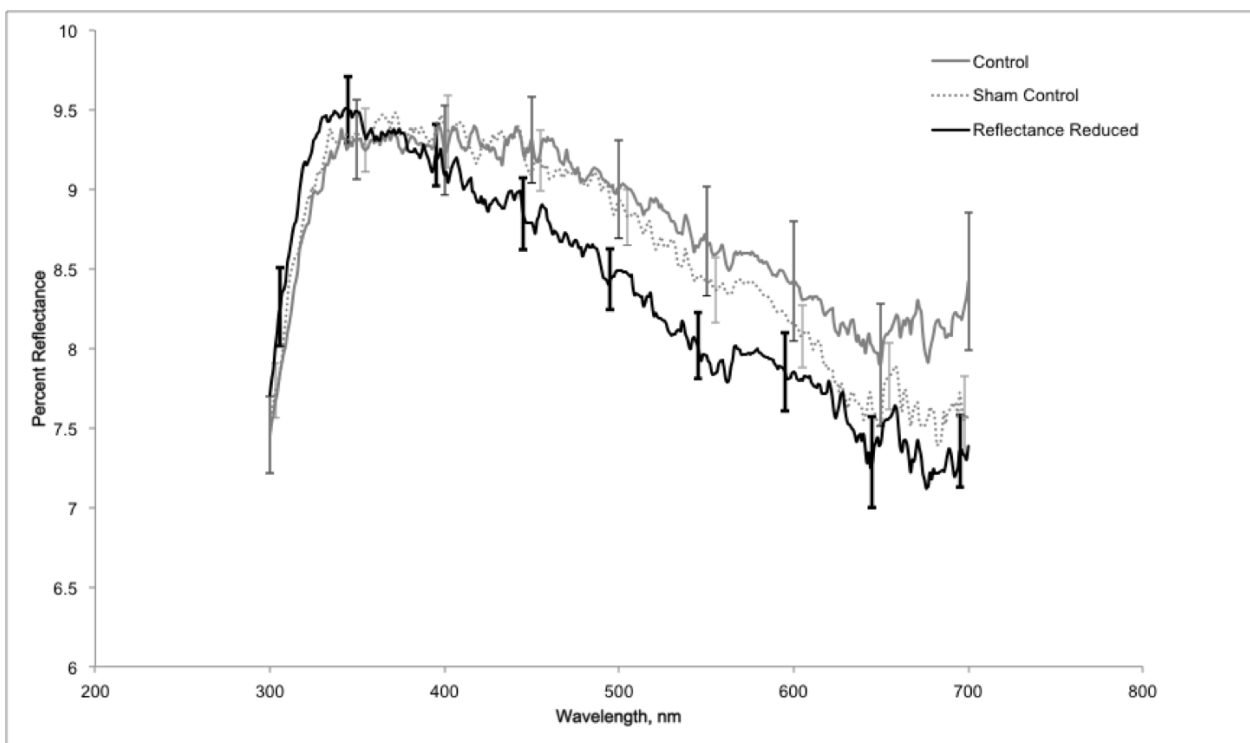
Figure 2.1. Mean reflectance and SE (per100 nm) of juvenile Florida scrub-jay rectrices with and without experimental plumage manipulations.

The experimental reduction treatment significantly reduced plumage reflectance, but the sham control treatment did not (Fig. 1). The mean ± standard error changes in mean brightness for the reflectance reduction and sham treatments were -1.12 ± 0.69 and -0.96 ± .52, respectively. Neither of these treatments had a significant effect on the mean brightness of feathers ($F_{2,\,30} =$

0.56, $p = 0.58$). Both UV chroma and hue, however, were significantly affected by plumage manipulation ($F_{2,30} = 21.52$, $p < 0.001$ and $F_{2,30} = 3.96$, $p = 0.03$, respectively). The reflectance reduction treatment caused a mean ± standard error change in UV chroma of -0.01 ± 0.002 and in hue of 74.33 ± 29.94. For the sham control treatment the mean ± standard error changes in UV chroma and hue were -0.006 ± 0.002 and 22.73 ± 16.71, respectively. The independent contrasts confirmed that the reduction treatment significantly reduced UV chroma ($t = -6.26$, $p < 0.001$) and shifted hue toward longer wavelengths ($t = 2.78$, $p = 0.009$), while the sham and control treatments did not differ in UV chroma ($t = -1.171$, $p = 0.25$) or hue ($t = 0.927$, $p = 0.36$).

During our experiment, we observed dominance interactions between juveniles in 45 family groups. We excluded seven of these groups from all analyses; six because we observed one or no interactions in the post-treatment observation period and one because a focal bird was found injured during the post-treatment observations. In total, we analyzed data from 38 groups. No significant year effect existed ($F_{2,33} = 0.05$, $p = 0.82$), thus data from 2009 – 2011 were combined and analyzed together. Manipulating plumage had a significant effect on change in proportion of interactions won ($F_{2,33} = 3.82$, $p = 0.03$) but sex did not ($F_{1,33} = 1.34$, $p = 0.25$). Individuals for whom reflectance was experimentally reduced suffered a decrease in the proportion of interactions won (Fig. 2). The independent contrasts confirmed that the reflectance reduction group suffered a significantly larger Δ proportion of interactions won ($t = -2.81$, $p = 0.008$). The Δ proportion of interactions won did not differ significantly between the unmanipulated and sham controls ($t = -1.47$, $p = 0.15$). No pre-existing differences in dominance ($F_{2,35} = 0.90$, $p = 0.41$), mean brightness ($F_{2,33} = 0.57$, $p = 0.57$), UV chroma ($F_{2,33} = 0.32$, $p = 0.72$), or hue ($F_{2,33} = 0.14$, $p = 0.86$) existed between the control, sham, and reflectance reduction treatment groups.
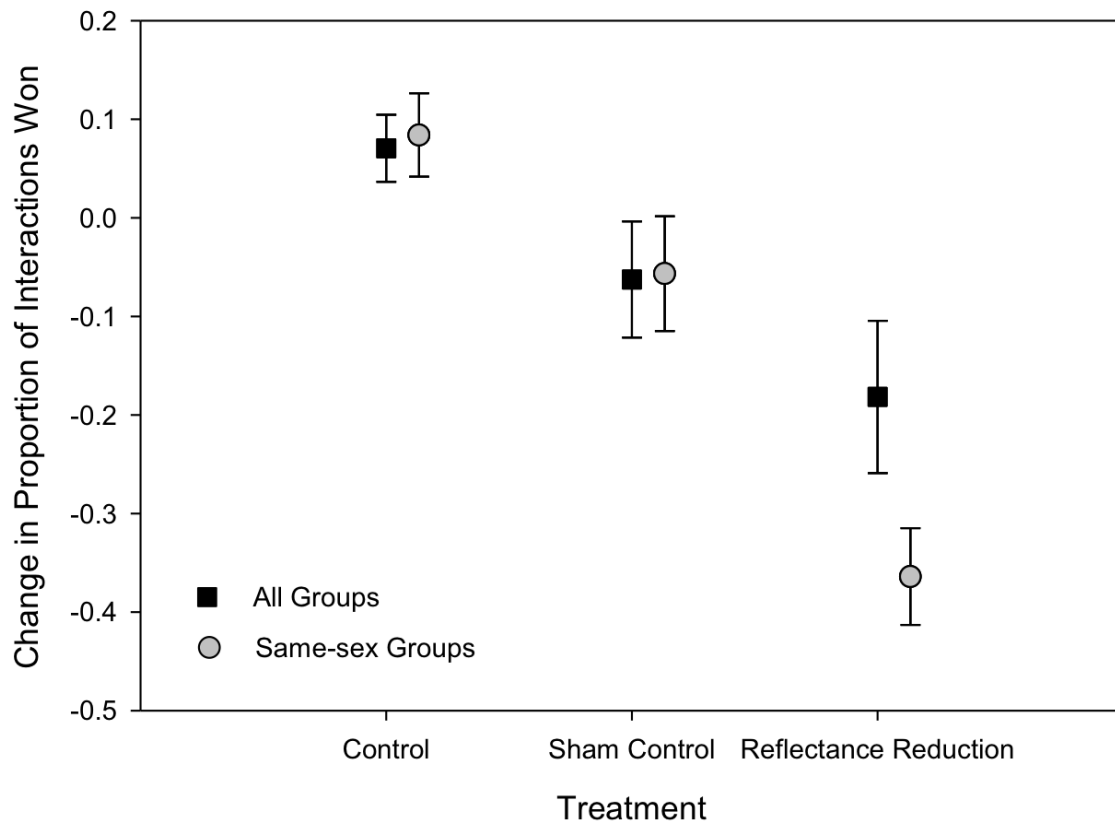
Figure 2.2. Mean and SE change in proportion of interactions won at a feeder by juvenile scrub-jays before and after plumage manipulation

Individuals were assigned to treatment groups irrespective of sex and males and females were not represented evenly across treatments. We culled our data further to include only the 23 dyads of same-sex siblings, 17 all female and 7 all male. We found that reducing reflectance caused a significant decrease in dominance ($F_{2, 19} = 23.04$, $p = 8.32$ x 10^{-6}, Fig. 2) in same-sex groups.

Discussion

Sexual selection is an unlikely explanation for the sexually dimorphic UV blue colouration of juvenile Florida scrub-jays. We used behavioral observations and a plumage manipulation experiment to test the hypothesis that this plumage colouration signals status among juveniles. Our results show that although no measure of plumage reflectance was associated with dominance, reducing UV chroma and increasing hue does cause a decrease in dominance. Although the individuals in the sham control treatment also experienced a decrease in dominance it was not significant and the decrease experienced by the reflectance reduced individuals was, indicating a true treatment effect. This change in dominance due to reflectance reduction supports our hypothesis that plumage colouration is used to signal status among juvenile Florida scrub-jay brood mates.

Among juveniles, males were more likely to be dominant to and have higher UV chroma than females, suggesting that UV chroma may signal sex, which is associated with dominance. This is consistent with patterns in adults, in which male Florida scrub-jays are both more dominant (Woolfenden and Fitzpatrick 1977) and have higher UV chroma (Bridge et al. 2008) than females. However it is important to note that individuals with higher UV chroma were not significantly more likely than expected by chance to be dominant.

Plumage may signal aggressiveness or willingness to fight (Maynard Smith & Harper 1988, Vedder et. al 2010) rather than true dominance. In our species, aggressiveness and dominance are related, such that dominant birds are both more likely to initiate aggressive interactions and to win them, so we do not make a distinction between aggressiveness and dominance. However, when subordinates initiate a series of interactions, they increase their probability of winning, suggesting that subordinates may successfully vary their aggressiveness

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with resource value (Enquist et. al 1985). Because proportion of interactions won by the dominant individual and proportion of interactions initiated by the subordinate individual are inversely proportional, we conclude that our reflectance-reduction treatment caused subordinates to perceive reflectance-reduced individuals as less dominant and increase their level of aggression in response.

We used a reflectance reduction experiment to determine if dampening the plumage signal could change an individual's dominance. Our reflectance reduction treatment significantly reduced UV chroma and shifted hue to longer wavelengths, but did not alter mean brightness. The reflectance of reduced feathers was within ± 1 SD of control feathers, indicating that reduction treatment did not inadvertently create abnormal-looking birds. Although no calculated component of reflectance predicted dominance, we observed a decrease in the dominance of treated individuals, indicating that UV chroma, hue, or both are associated with dominance. Multiple ornaments may convey different messages, be redundant, or vary in reliability (Moller & Pomiankowski 1993), and the different components of plumage colour can be related to different traits (Silva et. al 2008). In Florida scrub-jays UV chroma, hue, and brightness all may be involved in dominance signaling or each may convey different information. Although we cannot pinpoint which component of plumage reflectance signals dominance, we can refute the null hypothesis, that sexual dimorphism in juveniles is the result of a developmental constraint and not of any adaptive value. Rather, we demonstrate that plumage ornamentation functions as a signal of dominance in juveniles and that the dampening of the signal reduces an individual's dominance, at least during the period that the signal is reduced. The possibility that individuals regain their dominance status after the plumage manipulation ceased to be effective warrants future investigation.

Juveniles may perceive their reflectance-reduced sibling as less likely to defend the feeder and more likely to retreat if challenged, and increase their level of aggression in response. If plumage reflectance is an honest signal of either dominance or aggressiveness, then we might expect the suite of behaviours of dominant individuals to be the same, even after experimental reflectance reduction. However, individuals may use assessment strategies to approximate their position in the dominance hierarchy (Arnott and Elwood 2009). If subordinate siblings react to the dominant sibling's reflectance reduction by increasing their assertiveness the dominant individual may reassess its own status and submit to the challenges of its siblings.

Manipulating plumage can alter physiology, and this change is likely mediated by social feedback (Rubenstein and Hauber 200). Saffran et al. (2008) found that experimentally increasing the plumage ornamentation of male barn swallows caused an increase in testosterone. It is possible that reducing an ornament would have the opposite effect, causing a decrease in testosterone, reducing both aggression and dominance. The plumage manipulations in our experiment may have had a two-fold effect, where 1) treated individuals were perceived as less dominant, causing their siblings to initiate aggressive interactions more often, and (2) and treated birds receive increased aggression, causing a decrease in testosterone, an increase in corticosterone, or both, causing their levels of aggression or dominance to drop, resulting in an overall decrease in dominance status. Future research will examine changes in circulating testosterone and corticosterone as a result of plumage manipulation.

Although no component of plumage was consistently associated with dominance, males are both more likely to be dominant and to have higher UV chroma. It is possible that plumage signals sex and is thus associated with dominance but not necessarily signaling status per se. If this is the case, males within observed broods would be more likely to be chosen for

experimental plumage reflectance reduction simply because they tend to be dominant to females within their brood. The plumage manipulation treatment would cause their plumage to become more female-like and other males within the brood would then increase their assertiveness in response to the manipulation. Surprisingly, females were not under-represented in the control and reflectance reduction groups. Nine of the twelve control, six of the fifteen sham control, and nine of the fourteen reflectance reduction individuals were female. Uneven representation of sexes in the treatment groups may explain why we failed to detect an effect of sex on change in dominance. Nevertheless, when only siblings of the same sex were included in the analysis, reducing plumage reflectance still significantly decreased dominance. In this reduced data set, seven of the eight reflectance-reduced individuals were female, demonstrating that the dominance of females can be reduced by plumage manipulation. Therefore, we reject the idea that plumage colour is signaling sex and not status.

    We choose to observe dominance between same-aged siblings on their natal territories to control for the effect of territory ownership on dominance. Although we have demonstrated that juvenile plumage signals are important among siblings, they are likely to be much more important among juveniles from different territories. Juveniles make forays, often in large aggregations consisting of groups of siblings from several territories. Badges of status may be especially important in mediating encounters between unfamiliar individuals in these flocks. Alternatively, the large flocks may allow for direct observations of behaviour, providing additional information about status. Pinyon jays (*Gymnorhinus cyanocephalus*), which form large, complex groups, can use transitive inferences to estimate their dominance status relative to an unfamiliar bird observed interacting with a familiar one (Paz-y-Mino et. al 2004). Because an individual may have high reflectance relative to its siblings but not relative to the population,

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transitive inference may be used to calibrate signaling in flocks. Large groups of familiar and unfamiliar individuals may allow scrub-jays to use information from both status signals and transitive inference to decipher dominance relationships.

Helpers make frequent forays to neighboring territories as part of a stay-and-foray strategy of searching for breeding vacancies (Woolfenden and Fitzpatrick 1984). The interactions made within flocks as juveniles may influence the outcome of these adult competitions. In Florida scrub-jays the most influential determinant of fitness is whether or not an individual becomes a breeder (Fitzpatrick and Woolfenden 1988). Half of all males that obtain breeding territories do so by successfully out-competing other helpers in the neighborhood to replace a dead breeder (Woolfenden and Fitzpatrick 1984). Males may also compete directly with siblings to inherit all or a portion (territorial budding) of their natal territory, and it is likely that dominance relationships established among juveniles influence the outcomes of competition for these types of vacancies (Strickland 1991).

Signaling plays an important role in mediating social interactions. We have demonstrated that plumage reflectance is involved in status signaling among juvenile Florida scrub-jays. The relative influence of sexual and social selection on traits is likely to vary with the degree of sociality and mating system of a species. Status signaling may be more important in cooperative species where not all individuals breed and competition for breeding vacancies is intense. A more complete understanding of status signaling among juveniles can yield insights into variation in lifetime fitness among adults, especially in social systems with large asymmetries in lifetime reproductive success.

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CHAPTER THREE ~ SHARED GENES, SHARED ENVIRONMENTS: ESTIMATING HERITABILITY AND ENVIRONMENTAL EFFECTS ON PLUMAGE COLOUR IN A COOPERATIVE BREEDING BIRD[2]

Introduction

Sexually dimorphic coloration occurs in several taxa and numerous studies have demonstrated the selective advantages of bright coloration for mating success [1] and dominance-status signaling [2–4]. Sexually dimorphic coloration is particularly widespread in birds and the costs, benefits, and mechanisms of avian coloration have been well documented [5]. However, while the proximate and ultimate causes of bird coloration are relatively well understood, the genetic basis of colour variation has received relatively little attention [6].

Most plumage colors can be attributed to melanin pigments, carotenoid pigments, or the structure of the feather itself [7]. Melanin production is likely under genetic control [8] and the melanin-based black "tie" of great tits (*Parus major)* is highly heritable ($h^2 = 0.77 \pm 0.33$, Quesada and Senar 2009). Unlike melanin, carotenoids must be obtained from the diet [10] and studies of carotenoid-based colors (reds, oranges, yellows) found low heritability [9,11–13]. Short-wavelength feather colors are based on the structure of the feather cortex which scatters the light, reflecting back the short wavelength light [14] and both genetic and environmental factors contribute to variation in blue-UV colour [12,15].

However, most of these heritability estimates assume a strict autosomal genetic basis. This assumption is surprising because sex-linked inheritance of colour was documented as early as 1927 in guppies (P*oecilia reticulata)* [16], a finding that has been confirmed both by quantitative

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genetic ([17] and QTL studies ([18]. Sex-linked inheritance of colour also has been documented in other taxa [19,20], but few studies of colour heritability in birds consider sex-linkage [21].

Birds are a particularly interesting group in which to study the genetics of coloration because Z-linkage of female preference facilitates the evolution of conspicuous male secondary sexual traits under Fisher's runaway models of sexual selection [22]. Moreover, birds lack a global dosage compensation mechanism [23–26] and thus, quantitative genetic methods are well suited to partition autosomal and sex chromosome linked genetic variance [21].

Florida scrub-jays (*Aphelocoma coerulescens*) exhibit sexually dimorphic ultra-violet plumage coloration as juveniles [27] and adults [28]. In juveniles this colour is a signal of dominance status [29], but its function in adults is unknown. In addition to sharing genes, closely-related individuals of this species also share environments because dispersal distances are short and territories are usually inherited from father to son [30], making this species a particularly interesting subject for studies of heritability.

Here we use long-term data to examine the relative influence of genetic and environmental effects on plumage colour of juvenile Florida scrub-jays, if sex-linkage contributes to the observed sexual dimorphism in plumage coloration and, finally, whether plumage coloration is under selection in this population.

A trait's inheritance can reveal its evolutionary potential and suggest what selective forces may be operating. For example, sexually dimorphic traits are more likely to show patterns of sex-linked inheritance than monomorphic ones (Rice 1984). Striking, sexually dimorphic coloration occurs in several taxa, and numerous studies demonstrate the selective advantages of bright coloration for mating (Andersson 1994) and status signaling (Bradbury and Davies 1987; Berglund et al. 1996; Senar 2006). For these colorful traits to evolve, they must have a genetic

basis. However, it is difficult to determine if traits are due to genetic or environmental effects when relatives live in close proximity, thus sharing both genes and environments.

Sexually dimorphic coloration is widespread in birds. Considerable literature exists on the costs, benefits, and mechanisms of avian coloration (Hill and McGraw 2006a), and the proximate and ultimate causes of coloration are relatively well understood. In birds, females are the heterogametic sex, which facilitates good genes models of sexual selection (Kirkpatrick and Hall 2004). Moreover, unlike some taxa where sex-linked genes in the heterogametic sex are transcribed at double the amount as in the homogametic sex, birds lack global dosage compensation (Ellegren et al. 2007; Itoh et al. 2007; Arnold et al. 2008; Wolf and Bryk 2011). Thus, quantitative genetic methods are well suited to partition autosomal and sex chromosome linked genetic variance (Husby et al. 2013).

Avian coloration is studied extensively, but the genetic basis for its variation has received relatively little attention (Mundy 2005), and many of these heritability estimates assume a strict autosomal genetic basis (Fitze et al. 2003; Hadfield et al. 2006; Evans and Sheldon 2012). This assumption is surprising because sex-linked inheritance of color was documented as early as 1927 in guppies (P*oecilia reticulata)* (Winge 1927). This finding was expanded on when Houde (1992) found that guppies' orange coloration was Y-linked-and confirmed when Tripathi et al. (2009) mapped color QTL to the Y chromosome. Despite sex-linked inheritance of color also being documented in other taxa (amphibians: Miura et al. 2011; butterflies: Ellers and Boggs 2002) few studies of the heritability of avian color considered sex-linkage (but see Johnsen et al. 2003; Husby et al. 2013).

Based on existing research, we can make general predictions about the heritability of plumage coloration. Most plumage colors can be attributed to melanin pigments, carotenoid

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pigments, or the structure of the feather itself (Hill and McGraw 2006b). Melanin production is likely to be under genetic control (McGraw 2006b) and the melanin-based black tie of great tits (*Parus major)* is highly heritable ($h^2 = 0.77 \pm 0.33$, Quesada and Senar 2009). Unlike melanin, carotenoids must be obtained from the diet (McGraw 2006a) and carotenoid-based colors (reds, oranges, yellows) show low heritability (Fitze et al. 2003; Johnsen et al. 2003; Hadfield et al. 2006; Quesada and Senar 2009). Short-wavelength feather colors are based on the structure of the feather cortex which scatters the light, reflecting back the short wavelengths (Prum 2006). Blue and ultra-violet (UV) hues are a result of the keratin-based nanostructure of feathers, which the pigment melanin is a part (Prum 2006). However, even slight restrictions in diet can influence blue-UV color (Hill 2006). Both genetic and environmental factors contribute to variation of blue-UV color (Johnsen et al. 2003; Hadfield et al. 2007), as is expected from mechanisms of structural coloration.

Here we examine the relative influence of genetic and environmental effects on the plumage color of juvenile Florida scrub-jays (*Aphelocoma coerulescens*), if the observed sexual dimorphism in plumage coloration is due to sex-linkage, and whether it is under selection. Both adult (Bridge et al. 2008) and juvenile (Siefferman et al. 2008) Florida scrub-jays exhibit sexually dimorphic ultra-violet plumage coloration. In juveniles this color is a signal of dominance status (Tringali and Bowman 2012), but its function in adults is unknown. Because social dominance determines the outcome of competition for resources, and plumage coloration signals dominance in this species, we predict that selection will act via overwinter survival or whether or not a bird obtains breeder status.

Methods

Biology of Study Organism

Florida scrub-jays are a territorial, non-migratory, socially and genetically monogamous cooperative breeding species [30,31]. These characteristics allow us to follow individuals for the duration of their life and accurately determine parentage in the field. Many adults never breed, and among breeders reproductive skew is high; most (51%) breeding males produce no breeding offspring over their lifetime and less than 10% produce five or more. Florida scrub-jays disperse short distances and males frequently inherit all or part of their father's territory [30]. High reproductive skew coupled with short dispersal distance creates a pattern where highly successful lineages are often spatially clustered within the landscape.

Study population and data collection

Our work was conducted on the population of Florida scrub-jays long studied at Archbold Biological Station, Highlands County, Florida, USA (21° 10'N, 81° 21'W). All individuals in the population are marked with a unique combination of colour bands and each is monitored throughout its lifetime on the study area. Each year all nests are found, monitored, and their locations recorded with GPS.

Nestlings are banded with a single colour band and a blood sample is collected for genetic sex determination. These individuals are re-captured as juveniles, at approximately 65 d post-fledging, at which time they are given a unique set of colour bands and (since 1990) the outermost right rectrix is collected. Rectrices are stored in individually labeled envelopes in a museum cabinet in a climate-controlled room. UV-blue coloration does not fade over the timespans that our feather samples were in storage [27,32]. We used this historical collection of

rectrices in our analyses.

To measure feather reflectance we used an Ocean Optics USB-4000 spectrometer (Ocean Optics, Dunedin, FL) connected to a DH-200 deuterium halogen light source by a bifurcated fiber optic probe. We measured three 3.14 mm^2 points on each feather, 1, 2, and 3 millimeters from the distal tip by holding the probe at a 90° angle 0.5 cm from the surface of the feather. We averaged these three measurements for each sample and then calculated mean brightness $(\frac{\Sigma R_{\lambda_{300-700}}}{n_w})$, UV chroma $(\frac{\Sigma R_{\lambda_{300-700}}}{\Sigma R_{\lambda_{300-400}}})$, and hue $(\lambda_{R_{max}})$, where R is reflectance, λ is wavelength, and n$_w$ is number of wavelengths measured [33]. We had a total of 3534 measurements from 1178 individuals (three different colour measurements per individual, no repeated observations on the same individual, see Table 1).

Sexual dimorphism

Because we have a much larger sample size than previous studies of Florida scrub-jay colour [27–29], we used a two-way mixed effects ANOVA with sex as a fixed factor and year as a random factor to confirm that plumage is sexually dimorphic in juveniles. Following Lovich and Gibbons [34], we calculated the degree of sexual dimorphism (SD) using the ratio of the trait mean of the sex (μ) with the larger value to the trait mean of the sex with the smaller value so that $SD = \mu_{larger}/\mu_{smaller}$. The ratio is assigned a positive value if females had the larger trait value and negative if males had the larger value.

Pedigree information

We obtained information on coefficients of relatedness between individuals in this study from a pedigree reconstructed based on field observations [31]. In total the pedigree contained 1401 individuals, of which 249 maternities, 250 paternities, 2,016 full-sibling links, and 3866 half-sibling links were informative for analysis of coloration. Mean relatedness was 0.0054, and was estimated using the R-package pedantics [35].

Quantitative genetic analyses

To partition variation in mean brightness, UV chroma, and hue we used the above pedigree in a mixed model framework [36]. We first estimated the autosomal additive genetic basis of coloration (mean brightness, UV chroma, and hue) using the model:

$$\text{Trait} = \text{Sex} + V_A + V_M + V_T + V_R \tag{1},$$

where trait refers to the trait in question (mean brightness, UV chroma, or hue), sex is a two-level factor to account for the slight sexual dimorphism in coloration [27], and V_A is the additive genetic autosomal variance, V_M the maternal variance, V_T the variance due to territories, and V_R is the residual variance.

Second, we estimated the Z-linked genetic relatedness matrix to estimate the proportion of genetic variance located on the macro sex chromosome. The full details can be found in Husby et al. (2013) [21]. Briefly, we expanded on the model above such that variation in the colour traits was modeled as:

$$\text{Trait} = \text{Sex} + V_A + V_M + V_T + V_Z + V_R \tag{2},$$

where V_Z, represents sex linked genetic variance.

Sex-linked genetic variance can be separated from the autosomal genetic variance because

the Z-linked and autosomal relatedness coefficients differ between some types of relatives [37]. Because females are the heterogametic sex (ZW) in birds, male offspring inherit one of their two Z chromosomes directly from their mother and female offspring their single Z chromosome from their father. As a result, the relatedness coefficient between two male full siblings, for example, will be 0.75 for any Z-linked gene, compared to 0.5 for an autosomal gene. Some types of relatives have identical relatedness for both Z-linked and autosomal markers (e.g. father-son relationship), thus the power to detect Z-linked genetic variance is lower than for autosomal genetic variance [21].

Multivariate quantitative genetic models

Blue and ultra-violet plumage is structural [14] and therefore it is possible that the colour parameters we measured are not independent of each other. To examine this possibility, we ran multivariate models to test for phenotypic and genetic dependencies between the colour traits. Note that for the genetic model we only examined UV chroma and brightness because we could not detect any additive genetic basis to hue (Table 2); hence, a genetic correlation is not defined. Our bivariate phenotypic model was therefore:

$$\text{Trait1 Trait2} = \text{Sex} + V_I + V_M + V_T + V_R \tag{3},$$

where V_I is the between-individual variance. We extended this model to a bivariate animal model as:

$$\text{UV chroma Brightness} = \text{Sex} + V_A + V_M + V_T + V_R \tag{4}.$$

We did not consider sex-linked genetic correlation because we did not find statistical support for sex linkage of any trait and the estimated sex-linked genetic variance for brightness was zero.

We statistically tested variance components using Likelihood Ratio Tests (LRTs), which have a mixture of a χ^2 distribution with one degree of freedom (testing a single variance component) and a χ^2 distribution with null degrees of freedom, because of testing on the boundary of the parameter space [38]. To test the significance of the phenotypic and genetic correlation, we constrained the correlation to zero and compared the model to one in which the correlation was estimated. Note that because correlations (or more generally, covariances) need not be positive, these tests are χ^2 distributed with 1 degree of freedom. To facilitate model convergence, we multiplied the UV measurements by a factor of 100 [39] but report all estimates on their original scale. All quantitative genetic models were run using the software ASReml 3.0 [40].

Selection analyses

The importance of plumage coloration for social dominance has been well established in this system [29] but the strength of selection has not been estimated. Therefore, we used information on lifetime reproductive success to calculate non-linear selection gradients [41] using Generalized Additive Models (GAMs). We measured lifetime reproductive success as the number of breeding offspring produced, where breeding is defined as having produced at least one egg. Because approximately half of all breeding males never produce breeding offspring, this trait follows a Poisson distribution. We limited this analysis to the 2005 and earlier cohorts to exclude birds who still have several reproductive years ahead of them. Of the 602 individuals included in this analysis only 16 were still alive at the time of analysis. Colour traits were standardized to create z-scores and thus the reported estimates are standardized selection

gradients [42]. We used the R-package 'mgcv' to run the GAMs [43], with the colour variables as covariates and sex as factor.

Results

Sexual dimorphism

Juvenile males and females differed significantly in mean brightness ($F_{1, 1048} = 26.443$, p < 0.0001), UV chroma ($F_{1, 1047} = 43.732$, p < 0.0001), and hue ($F_{1, 1048} = 18.354$, p < 0.0001). Compared to females, males had plumage with lower mean brightness that is more UV-shifted (Table 1). However, despite differing significantly in all components of plumage reflectance, the sexual dimorphism 'score'/parameter/or similar was low, with ratios close to one (Table 1).

Quantitative genetic basis of trait coloration

We found that both mean brightness ($h^2 = 0.382 \pm 0.079$, $\chi^2 = 32.1$, p < 0.001) and UV chroma ($h^2 = 0.250 \pm 0.084$, $\chi^2 = 12.4$, p < 0.001) were moderately heritable. This is in contrast to hue, which displayed no genetic variance (Table 2). Because of the observed sexual dimorphism in plumage coloration in this species (Table 1) and theoretical work predicting that the evolution of sexual dimorphism is facilitated by sex-linked genetic variance (Rice 1984), we examined if this was the case here. However, we found no support for this: the sex linked heritability estimate for mean brightness, h^2_z, was zero ($\chi^2_1 = 0$, p $= 0.5$) and for UV chroma was 0.057, which did not differ significantly from zero ($\chi^2_1 = 0.38$, p $= 0.27$). Sex linkage of hue was not examined because we found no genetic variance in this trait. Although small and non-significant, the addition of sex-linked genetic variance decreased the estimated autosomal heritability from 0.250 to 0.194, an appreciable difference (Table 3).

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In addition to estimating additive genetic variance, we also estimated the influence of territory and non-genetic maternal effects on the colour components. Territory explained a relatively small proportion of the variance in mean brightness and UV chroma, and had no effect on hue (Table 2). Interestingly, maternal effects were relatively strong, explaining 10-25% of the variance of mean brightness, UV chroma, and hue (Table 2).

Table 3.1: Least squares means ± standard error of colour traits in juvenile male and female Florida scrub-jays. Males and females differ significantly (p < 0.0001) in all measures of reflectance, but sexual dimorphism slight.

Sex	Mean Brightness	UV chroma	Hue
Female	9.326 ± 0.226	0.282 ± 0.007	396.822 ± 6.458
Male	9.039 ± 0.226	0.289 ± 0.007	388.626 ± 6.456
Sexual Dimorphism	1.032	-1.025	1.021

Table 3.2: Variance partitioning and the proportion of variance explained (PVE) of colour traits in Florida scrub-jays, assuming an autosomal additive genetic basis of the trait.

Trait	Territory (SE)	Dam (SE)	Va (SE)	Vp (SE)	PVE: Natal Territory (SE)	PVE: Maternal Effects (SE)	PVE: h^2_A (SE)
Mean brightness	$0.717E^{-01}$ $(0.734E^{-01})$	0.531 (0.110)	0.796 (0.181)	2.082 (0.131)	0.034 (0.035)	0.255 (0.046)	0.382 (0.079)
UV chroma	$0.139E^{-03}$ $(0.615E^{-04})$	$0.306E^{-03}$ $(0.727E^{-04})$	$0.324E^{-03}$ $(0.112E^{-03})$	$0.130E^{-02}$ $(0.815E^{-04})$	0.107 (0.045)	0.236 (0.051)	0.250 (0.084)
Hue	$0.822E^{-04}$ $(0.395E^{-05})$	230.10 (60.237)	$0.119E^{-03}$ $(0.571E^{-05})$	1946.9 (88.275)	0	0.118 (0.029)	0

Table 3.3: Variance partitioning of colour traits in Florida scrub-jays, assuming sex linked genetic variance. In general, there was little support for Z linked variance of the different colour traits in this species.

Trait	Territory (SE)	Dam (SE)	Va (SE)	Vz (SE)	Vp (SE)	h^2_A (SE)	h^2_z (SE)
Mean brightness	$0.717E^{-01}$ $(0.734E^{-01})$	0.531 (0.110)	0.796 (0.182)	$0.233E^{-06}$ $(0.374E^{-07})$	2.082 (0.131)	0.382 (0.079)	0
UV chroma	$0.141E^{-03}$ $(0.616E^{-04})$	$0.310E^{-03}$ $(0.732E^{-04})$	$0.255E^{-03}$ $(0.142E^{-03})$	$0.749E^{-04}$ $(0.103E^{-03})$	$0.132E^{-02}$ $(0.872E^{-04})$	0.194 (0.109)	0.0569 (0.077)

Multivariate genetic basis of trait coloration

All colour traits were significantly negatively correlated on the phenotypic level with correlations ranging from -0.084 between mean brightness and UV chroma to -0.536 between hue and UV chroma (Table 4). On the genetic level we could only test the correlation between mean brightness and UV chroma because we did not find any indication of a genetic basis to hue (Table 2). We found support for a strong negative genetic correlation between UV chroma and brightness in this population (sex corrected: -0.084, $p < 0.001$; autosomal: -0.821, $p < 0.001$) (Table 4).

Table 3.4: Phenotypic and genetic correlation estimates between colour measures. Phenotypic correlations (sex corrected) are in the upper triangular and (autosomal) genetic correlations in the lower triangular, SE in parentheses. Note that genetic correlations between hue and other traits were not estimable since no genetic variance was found for hue (see Table 1).

	Mean brightness	UV chroma	Hue
Mean brightness	-	-0.084 (0.031)**	-0.240 (0.029)
UV chroma	-0.821 (0.177)***	-	-0.536 (0.022)
Hue	NA	NA	-

Selection on trait coloration

Given the importance of plumage coloration in establishing social dominance in this species and that dominance likely influences territory acquisition, we next examined selection on mean brightness, UV chroma, and hue. When both sexes were analyzed together, only mean brightness ($\chi^2_{6.81} = 37.89$, $p < 0.0001$) was significantly related to lifetime reproductive success, but this model only explained 5.86% of deviance. Sex was significant in all three models. Models were re-run separately for males and females. Mean brightness was significantly related to lifetime reproductive success for both males ($\chi^2_{8.92} = 22.43$, $p < 0.007$, deviance explained =

4.89%) and females ($\chi^2_{8.25}$ = 52.14, p < 0.0001, deviance explained = 10.2%) so that individuals with lower mean brightness showed higher lifetime reproductive success (Figure 1). UV chroma was not significantly related to lifetime reproductive success for either sex, although for males there was a trend toward stabilizing selection (Figure 1). Female hue was significantly related to lifetime reproductive success ($\chi^2_{4.74}$ = 13.34, p < 0.03, deviance explained = 4.42%), but male hue was not. Lifetime reproductive success was lower for females with shorter wavelength (more UV-shifted) hues, but was not associated with hue in males (Figure 1).
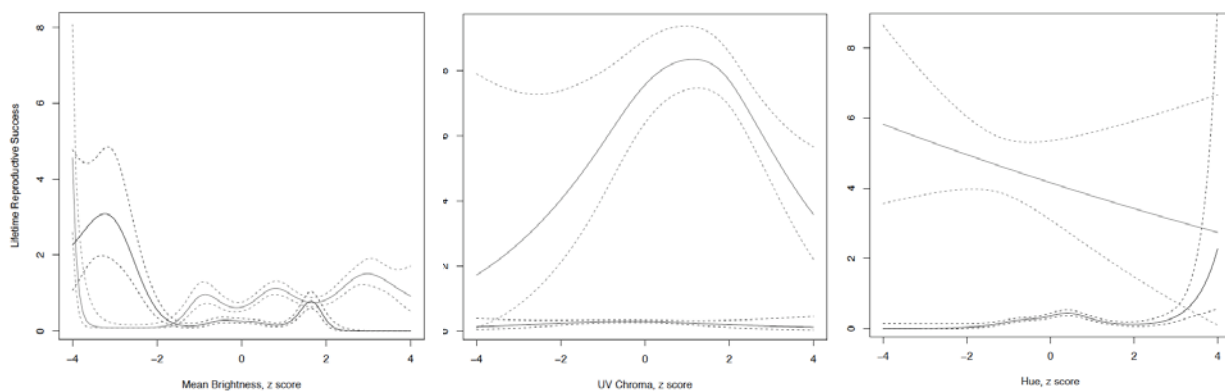
Figure 3.1. Predicted selection gradients ± standard error for mean brightness, UV chroma, and hue in Florida scrub-jays. Predictions for females are shown in black and males in grey.

Environmental basis of trait coloration and maternal effects

In addition to estimating additive genetic variance, we also estimated the influence of territory and non-genetic maternal effects on the color components. Territory explained a relatively small proportion of the variance in mean brightness and UV chroma, and had no effect on hue (Table 1). Maternal effects were relatively strong, explaining 10-25% of the variance of mean brightness, UV chroma, and hue (Table 1).

Discussion

In species where relatives share both genes and environments, separating genetic and environmental effects can be difficult, but crucial to determining if the traits of certain lineages are due to genetic or environmental factors. Here we estimated the relative influences of genetics and environment on three components of juvenile plumage colour in Florida scrub-jays. Both mean brightness and UV chroma were moderately heritable, but without evidence of sex-linked inheritance. A substantial part of the variation in UV coloration was due to environmental effects, in particular maternal effects with little effect of natal territory. Our heritability estimates are substantially higher than those for blue-UV plumage colour in blue tits (*Cyanistes caeruleus*) [12,15].

Plumage patterns are frequently sexually dimorphic [5], and one way sexual dimorphism might arise is if the genes underlying these traits are sex linked [22,44]. Despite early evidence of such a mechanism in guppies [16], this has rarely been explored in other systems [but see 19–21]. In Florida scrub-jays, the sexes are monomorphic to the human eye, but are dimorphic in the UV spectrum (Table 1). Despite theoretical work suggesting that the evolution of such dimorphism will be facilitated if genes for these traits are sex linked, we found no evidence of significant sex-linked inheritance for any component of plumage colour (Table 3). Moreover, the estimated sex-linked heritability was also rather low ($h^2_z = 0.057$). Although sex-linked inheritance of sexually dimorphic plumage colour has been documented in other species [21], it is perhaps unsurprising that we have found no evidence of it in the Florida scrub-jay because sexual dimorphism is relatively minor (Table 1, [28]).

Rice (1984) hypothesized that sexually antagonistic genes would accumulate on the sex chromosomes, but the optimum brightness and chroma of plumage is unlikely to differ between

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male and female scrub-jays. Unlike colour in guppies, where the advantage of being a brightly colored male is countered by the costs of higher predation risk [45], colour in scrub-jays does not carry such a high price; thus, the optima for both sexes should be similar. Additionally, sexual dimorphism is expected to increase with increasingly promiscuous mating systems [46], and Florida scrub-jays are monogamous [31] and although both adult and juvenile scrub-jays show dimorphic coloration, this difference is rather slight compared to the extreme sexual dimorphism observed in many other species. Furthermore, with the exception of hue, for which no additive genetic variance was detected, selection is not driving the evolution of different colour optima for the sexes.

Because plumage colour signals social dominance in juvenile Florida scrub-jays [29], and dominant individuals may have priority access to resources including breeding territories, natural selection may operate via lifetime reproductive success. It is important to note that in Florida scrub-jays individuals that survive long enough eventually become breeders, but breeding earlier in life confers a significant fitness advantage. Because of this pattern, lifetime reproductive success also has a survival component. Mean brightness and female hue were related to lifetime reproductive success, but UV chroma and male hue were not. The relationship between mean brightness and lifetime reproductive success does not differ between the sexes; individuals with less bright plumage have higher reproductive success. Selection is not acting on the hue of males, but is selecting for less UV-shifted hues in females. However, hue is not heritable, thus sex-specific optima for hue will not evolve.

Territory had little if any effect on plumage reflectance. Because plumage reflectance signals social dominance and is unaffected by natal territory, jays from poor quality territories may be as competitive for territories and or breeding vacancies as those from higher quality

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territories. If this is the case, males from territories in poor habitat need not be resigned to inherit their father's low-quality territory and instead may benefit from competing for a vacancy left upon the death of a breeder at another territory in higher-quality habitat.

Maternal effects were strong. Although food limitation affects UV plumage, more recently Peters et al. [47] suggested that UV coloration might be more related to stress than to body condition. In Florida scrub-jays, nestlings whose mothers spent more time further from the nest had higher levels of the stress hormone corticosterone, and nest attendance behavior was highly variable among females [48]. Maternal effects on UV coloration may be mediated via nestling stress response to female incubation and provisioning behavior.
Understanding patterns of heritability is critical to understanding how traits evolve. We showed that mean brightness and UV chroma of juvenile Florida scrub-jay feathers is heritable, and strongly influenced by maternal effects. That a plumage pattern closely linked to social dominance shows heritability suggests that social dominance behaviors also may have a heritable component. In the last decade, much attention has been paid to so-called behavioral syndromes [49,50]. Estimating the heritability of these, as well as lifetime reproductive success, is an exciting avenue for exploration.

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CHAPTER FOUR ~ AN UNEXPECTED CONSEQUENCE OF URBANIZATION: FLORIDA SCRUB_JAYS FROM A SUBURBAN SITE HAVE MORE UV-SHIFTED PLUMAGE THAN THOSE FROM A WILDLAND SITE[3]

Introduction

Human activities alter regional landscapes and local habitats, which affect how animals perceive their environments (Van Dyck, 2012). An animal's perception of its environment can influence dispersal and habitat selection (Pasinelli and Walters, 2002; Schlaepfer et al., 2002), foraging (Brown and Kotler, 2004), and social interactions (Wong, 2012), which in turn can alter demographic rates and subsequent population trends. Urbanization is one of most ubiquitous ways humans modify the environment and more than half of the human population lives in urban areas, and these areas are expected to absorb the majority of the growing population (*World Urbanization Prospects: The 2011 Revision*, 2012). Urbanization fragments and degrades habitat and alters disturbance regimes, predator communities, and food availability. These changes to the environment may induce behavioral changes in animals, altering the demography of populations in and around urbanized areas.

Urbanization can simultaneously increase and decrease food resources for birds (Chace and Walsh, 2006). Human-provided foods are often abundant and ubiquitous; an estimated 45-50% of US households feed birds each year (Jones and Reynolds, 2008). Adult birds may benefit from anthropogenic sources of food (Auman et al., 2008; Olea and Baglione, 2008), such as bird or pet food, and garbage. However, nestlings suffer from the reduced arthropod abundance associated

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[3] Prepared as: Tringali, A. and R. Bowman. An unexpected consequence of urbanization: Florida scrub-jays from a suburban site have more UV-shifted plumage than those from a wildland site.

with urbanization because they require easily digestible, protein-rich food (Chamberlain et al., 2009; Shawkey et al., 2004). Even nestlings of omnivorous or urban adapted species may do poorly because of diet changes. For example, both American crow (*Corvus brachyrhynchos*) and European starling (*Sturnus vulgaris*) nestlings decreased in mass along rural-urban gradients (Heiss et al., 2009; Mennechez and Clergeau, 2006).

Our study species, the Federally Threatened Florida scrub-jay (*Aphelocoma coerulescens*), is endemic to Florida and approximately 30% of the extant population lives in suburban areas. Florida scrub-jays quickly acclimate to human presence. They frequent bird feeders and some are bold enough to take food directly from people's hands. This affability endears them to the residents of suburban neighborhoods, who readily provide them with peanuts and other foods. As a result, human-provided foods make up a large portion of the suburban scrub-jay diet. In the suburbs, anthropogenic foods are included in the nestling diet (Sauter et al., 2006), but in unaltered habitat nestlings are fed exclusively arthropods (Stallcup and Woolfenden, 1978). Although these human-provided foods are not appropriate for nestlings, parents feed them to nestlings when their abundance is high and natural foods are scarce (Sauter et al., 2006), which are the conditions observed in the suburbs. As young approach nutritional independence, they begin incorporating plant foods into their diets, either because they because as their growth rate slows (Woolfenden, 1978) they longer require quickly digestible food to fuel rapid growth, or because digestive efficiency increases with age (Batal and Parsons, 2002) and they are better able to digest foods that require longer gut retention time. Most feather growth occurs after nestlings have fledged, and during this time human-provided foods may be used to fuel feather development (Woolfenden, 1978).

Plumage color in Florida Scrub-Jays is related to condition (Siefferman et al., 2008) and

signals dominance among juveniles (Tringali and Bowman, 2012). Ornamental traits, such as plumage color, are considered honest advertisements of fitness because they are dependent on body condition (Kodric-Brown and Brown, 1984). However, the changes in food availability associated with urbanization can weaken the relationship between plumage coloration and body condition, degrading the advertisement's honesty. For example, in northern cardinals (*Cardinalis cardinalis*) the relationship between plumage brightness and body condition is weaker in suburban areas (Jones et al., 2010). If the relationship between body condition and plumage coloration is relaxed, plumage color may cease to be a valuable indicator of male quality, disrupting the processes of sexual section and assortative mating (Jones et al., 2010). In many species, mate choice is adaptive and more attractive mates may provide tangible benefits, such as higher parental care (Johnstone, 1995). If ornamentation no longer accurately reflects male quality, nestlings may receive reduced care, resulting in lower demographic rates in urbanized populations. We compared body and plumage condition, their relationship, and the use of plumage color as a signal of dominance between a suburban and a wildland population of Florida scrub-jays.

Methods

Study Sites and Populations

We compared a wildland population of jays at Archbold Biological Station to a suburban population at the Placid Lakes Estates subdivision, 10 km away. Archbold Biological Station is a privately owned preserve, where scrub is managed using prescribed fire (for a complete description see Woolfenden and Fitzpatrick 1985). Placid Lake Estates is a suburban housing

division, consisting of homes embedded in a matrix of fragmented and overgrown scrub habitat (for a complete description see Bowman and Woolfenden 2001). Arthropod abundance is lower, nestlings grow more slowly and fledge at lighter masses (Sauter 2005), and both brood reduction and post-fledging mortality is higher at the suburban study site (Bowman, 1998; Shawkey et al., 2004).

The demography of the wildland population has been studied since 1969 and that of the suburban population since 1991. As part of these long-term studies, all jays are individually marked with a unique combination of colored bands, all nests within the study areas are found and monitored, and morphometrics are measured for individuals 11 d post-hatch and again as nutritionally independent juveniles (~85 d post-hatch), at which time the outermost right rectrix is also collected. For this study, we used data from the 2008 and 2009 cohorts, giving us a sample of 68 Florida scrub-jays. These years were chosen because they are the only years for which dominance behavior was observed at both sites.

Spectroscopy & Ptilochronology

To measure plumage reflectance, we used an Ocean Optics USB-4000 spectrometer (Ocean Optics, Dunedin, FL) connected to a DH-2000 deuterium halogen light source by a bifurcated fiber optic probe. We averaged measurements from three 3.14 mm^2 circles on each feather sample to produce a single reflectance curve for each feather. From this curve we calculated mean brightness, UV chroma, and hue (Montgomerie, 2006).

Growth bars are visible light and darks bands on a feather. Each pair of dark and light bands represents 24 h of feather growth (Grubb, 1989). Like tree rings, these growth bars can be used to measure growth rates. Wider growth bars indicate faster feather growth. To measure

growth bar width we used the method described by Grubb (1989). We taped each rectrix to an index card and then used an insect pin to puncture the card at the proximate and ultimate ends of the feather and the growth bars. Then we removed the feather from the card, and used digital calipers to measure the length of the feather, as marked by the pinholes. Then we measured the ten growth bars centered on the point two-thirds the length of the feather from the proximate end, and divided this number by 10 to calculate average growth bar width.

Behavioral Observations

To determine patterns of within-brood dominance in both habitats, we observed same-aged siblings interacting at a feeder placed on their natal territories (Tringali and Bowman, 2012; Woolfenden and Fitzpatrick, 1977). Prior to beginning our observations, we trained individuals to retrieve peanut bits from a gravity feeder with a small opening that allowed only one bird to access peanuts at a time. Once all juveniles on a territory would reliably use the feeder, we began recording observations using a digital camcorder mounted on a tripod. Observations were ended when the juveniles ceased to return to the feeder after caching. Video recordings were watched in the lab and all aggressive interactions and the identities of the individuals involved were recorded. For each dyadic interaction, the aggressor was assigned a "win" and the receiver a "loss". Groups were observed until a linear hierarchy could be determined.

Statistical Analysis

To compare the morphometrics, color variables, and condition between juveniles in wildland and suburban habitat, we used ANOVAs with habitat, year, and their interaction included in the models. With the exception of hue, the residuals of for all models were normally

distributed. Transformations did not normalize the distributions for the residuals of hue, so we used untransformed values for all analyses. We used residuals from the regression of mass on tarsus measured at day 11 ($R^2_{adj} = 0.71$, $p < 0.0001$, $n = 68$) as an index of nestling body condition. For juvenile condition, we first used principal components analyses to collapse head breadth, head length, tarsus length, and wing chord measured at independence ($n = 68$) into two principal components. Component one, which was positively correlated most strongly with head length (0.92), head breadth (0.86), tarsus (0.73), and wing chord (0.60), explained 62.1% (eigenvalue $= 2.48$) of the variation in skeletal size. Component two also was correlated strongly with wing chord (0.76) and tarsus (-0.47) and explained 20.1% (eigenvalue $= 0.80$) of the variation in skeletal size. Then we used multiple regression to express mass as a function of skeletal size ($R^2_{adj} = 0.56$, $p < 0.0001$, $n = 56$). Because of the allometric relationship between body size and mass, we log transformed mass and skeletal size for this analysis. Both principle components had negative values, so we added constants to the components of skeletal size (5 and 1.5, respectively). Log transformations did not improve the fit of the regression of nestling mass on size, so we used untransformed values.

We used ANCOVAs to determine if plumage color is related to (a) body condition or (b) growth bar width and if these relationships differed between habitats and years. Initially we ran these models as full-factorials, but no three-way interactions were significant, so we present only main effects and the interaction between habitat and condition. We completed these analyses using JMP (SAS Institite , Inc., Cary, NC).

To determine if dominant individuals were more likely than expected by chance to be ranked first for any of the three color variables we used binomial tests. Sibling groups were broken into dyads and each member of the dyad was ranked for the color variables and

dominance. If the most dominant bird was also ranked first for the color variable, the dyad was counted as a success. Then using a probability of 0.5, we calculated the binomial z-ratios for suburban and wildland birds separately using R.

Results

No differences existed in mass, condition, or tail length between suburban and wildland individuals (Table 1). Mean brightness, UV chroma, and hue differed significantly by year and by habitat, but their interaction was not significant (Table 1). Suburban birds had lower mean brightness, but higher UV chroma and lower hue, indicating more UV-shifted color (Figure 1). Growth bar width did not differ with habitat or year (Table 1).
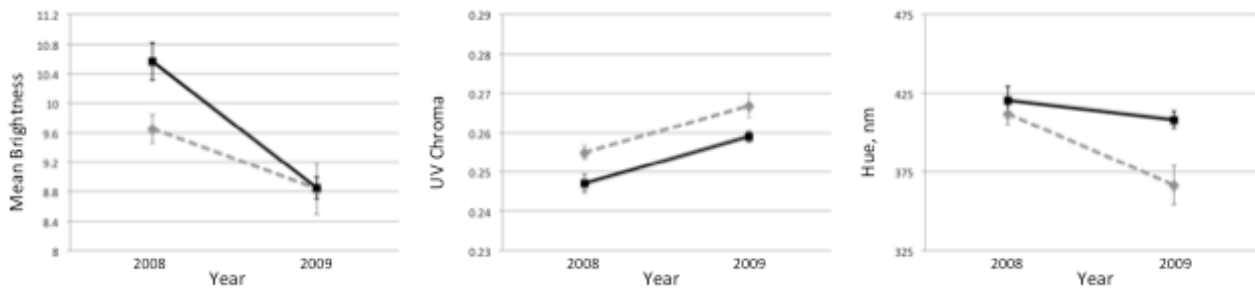
Figure 4.1. Mean ± SE of mean brightness, UV chroma, and hue for suburban and wildland Florida scrub-jay juveniles.

Neither nestling nor juvenile condition was significantly related to any measure of feather color. Mean brightness, UV chroma, and hue were not significantly dependent on nestling or juvenile condition (Table 2). However, when juvenile condition was used in these models, the habitat and year differences only remained significant for UV chroma and hue. Habitat and year were significant in all models using nestling condition. Growth bar width was not related to any component of color (Table 3).

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Table 4.1. Morphometric, color, and condition differences between a suburban and a wildland population of Florida scrub-jay juveniles.

Variable	Term	Df	MS	F-ratio	p-value
Nestling Mass	Habitat	1	38.35	0.88	0.35
	Year	1	49.30	1.14	0.29
	Habitat*Year	1	12.29	0.28	0.60
	Error	64	43.40		
	Total	67			
Juvenile Mass	Habitat	1	0.48	0.02	0.88
	Year	1	44.17	2.22	0.14
	Habitat*Year	1	25.66	1.29	0.26
	Error	64	19.89		
	Total	67			
Tail Length	Habitat	1	73.57	3.28	0.08
	Year	1	9.81	0.44	0.51
	Habitat*Year	1	11.86	0.53	0.47
	Error	64	22.45		
	Total	67			
Mean Brightness	Habitat	1	3.06	4.28	**0.04**
	Year	1	20.20	28.21	**<0.0001**
	Habitat*Year	1	2.89	4.04	0.05
	Error	64	0.72		
	Total	67			
UV Chroma	Habitat	1	0.00085	14.96	**0.003**
	Year	1	0.0017	30.31	**<0.0001**
	Habitat*Year	1	1.24e-8	0.0002	0.99
	Error	64	0.00006		
	Total	67			
Hue	Habitat	1	7322.94	7.75	**0.007**
	Year	1	9765.60	10.34	**0.002**
	Habitat*Year	1	3315.37	3.51	0.066
	Error	63	944.75		
	Total	66			
G bar	Habitat	1	0.002	0.02	0.89
	Year	1	0.02	0.29	0.59
	Habitat*Year	1	0.11	1.25	0.27
	Error	59	0.08		
	Total	62			
Nestling Condition	Habitat	1	12.46	1.02	0.32
	Year	1	5.43	0.44	0.51
	Habitat*Year	1	5.24	0.43	0.51
	Error	64	12.20		
	Total	67			
Juvenile Condition	Habitat	1	4.03e-4	1.24	0.27
	Year	1	3.94e-4	1.21	0.28
	Error	53	3.25e-4		
	Total	55			

In the wildlands, dominant juveniles were more likely to have higher mean brightness

than subordinates (one-tailed binomial test: n = 25, p = 0.02), but this was not true in the suburbs

(one-tailed binomial test: n = 14, p = 0.97). However, neither UV chroma nor hue was associated

with dominance in either the suburbs (one-tailed binomial tests: n = 15, p = 0.5; n = 12, p = 0.81)

or wildlands (one-tailed binomial tests: n = 24, p = 0.97; n = 24, p = 0.15).

Table 4.2. The relationships between color variables, habitat, and body condition of nestling and juvenile Florida scrub-jays from a suburban and a wildland site.

Response	Term	Df	MS	F-ratio	p-value
Mean Brightness	Habitat	1	4.22	5.55	**0.02**
	D11 Condition	1	0.09	0.11	0.74
	Habitat * D11 Condition	1	0.55	0.72	0.40
	Year	1	26.96	35.49	**< 0.0001**
	Error	63	0.76		
	Total	67			
UV Chroma	Habitat	1	0.0008	14.56	**0.0003**
	D11 Condition	1	4.0e-6	0.06	0.80
	Habitat * D11 Condition	1	3.4e-6	0.06	0.81
	Year	1	0.002	32.25	**< 0.0001**
	Error	63	5.7e-5		
	Total	67			
Hue	Habitat	1	5781.09	5.71	**0.02**
	D11 Condition	1	6.82	0.0067	0.93
	Habitat * D11 Condition	1	12.94	0.01	0.91
	Year	1	7324.39	7.23	**0.009**
	Error	62	1012.99		
	Total	66			
Mean Brightness	Habitat	1	1.90e-4	0.0002	0.99
	Juv Condition	1	7.76e-5	0.0001	0.99
	Habitat * Juv Condition	1	0.008	0.01	0.92
	Year	1	2.87	3.76	0.06
	Error	51	0.76		
	Total	55			
UV Chroma	Habitat	1	3.15-4	5.02	**0.03**
	Juv Condition	1	9.72e-5	1.55	0.22
	Habitat * Juv Condition	1	3.37e-6	0.05	0.82
	Year	1	7.0e-4	11.60	**0.001**
	Error	51	6.3e-5		
	Total	55			
Hue	Habitat	1	7119.00	6.63	**0.01**
	Juv Condition	1	1537.58	1.43	0.24
	Habitat * Juv Condition	1	798.49	0.74	0.39
	Year	1	9477.26	8.83	**0.005**
	Error	50	1073.89		
	Total	54			

Table 4.3. The relationships between color and growth bar width of Florida scrub-jay juveniles from a suburban and a wildland site.

Response	Term	Df	MS	F-ratio	p-value
Mean Brightness	Habitat	1	4.31	6.28	**0.02**
	Growth Bar	1	0.65	0.95	0.33
	Year	1	18.63	27.10	**< 0.0001**
	Habitat * Growth Bar	1	0.06	0.09	0.77
	Habitat * Year	1	3.63	5.28	**0.03**
	Year * Growth Bar	1	0.06	0.09	0.76
	Error	56	0.69		
	Total	62			
UV Chroma	Habitat	1	7.96e-4	13.54	**0.0005**
	Growth Bar	1	2.09e-5	0.36	0.55
	Year	1	1.57e-3	26.74	**< 0.0001**
	Habitat * Growth Bar	1	9.03e-5	1.54	0.22
	Habitat * Year	1	2.83e-8	0.0005	0.98
	Year * Growth Bar	1	4.83e-5	0.82	0.37
	Error	56	5.9e-5		
	Total	62			
Hue	Habitat	1	6913.56	6.88	**0.01**
	Growth Bar	1	17.54	0.02	0.90
	Year	1	9570.17	9.53	**0.003**
	Habitat * Growth Bar	1	89.02	0.09	0.77
	Habitat * Year	1	2428.06	2.42	0.13
	Year * Growth Bar	1	465.34	0.46	0.50
	Error	55	1004.49		
	Total	61			

Discussion

The morphometrics of nestling and juvenile Florida scrub-jays did not differ between the two habitats we studied. Previous research found differences in nestling mass between sites (Shawkey et al., 2004), and these differences do exist. However, our study only analyzed data from individuals surviving to nutritional independence. The smallest suburban nestlings do not survive to nutritional independence, and the suburban site has higher post-fledging mortality (Bowman, 1998). Our analysis obscured size differences that exist between suburban and wildland nestlings because it only included juveniles surviving to independence.

Despite the lack of differences in body mass or condition, we did detect significant habitat differences in all three measures of color. Suburban birds had lower mean brightness, but higher UV chroma, and shorter wavelength hue indicating less bright, but more UV-shifted feather color. Despite these differences in color, we saw no difference in feather growth between suburban and wildland juveniles, which suggests suburban birds may be able to produce feathers that reflect more short wavelength light (higher UV chroma and lower hue) with the same amount of investment in feather growth. No relationship exists between growth bar width and feather color, which supports this conclusion. As juveniles approach nutritional independence plant foods, such as peanuts, become more suitable. At the suburban site, the ability to exploit a new and essentially unlimited food that is high in both fat and protein may explain how these birds are able to compensate for lighter nestling mass and produce more UV-shifted feather color.

Neither the nestling nor juvenile condition indices were significant predictors for any of the three color measurements, indicating color is not related to condition in the wildlands or the suburbs (but see Siefferman et. al 2008). Although condition-dependence is a frequently invoked mechanism by which honest signaling is maintained, experimental evidence for this phenomenon is sparse. Evidence for the condition-dependence of structural plumage color is mixed, and Peters et al. (2011) suggest that variation in UV-coloration may be related to stress rather than condition. Suburban Florida scrub-jay adults have lower baseline corticosterone than wildland jays (Schoech et al., 2007), and the young may follow a similar pattern. Nestling corticosterone levels are influenced by maternal provisioning and nest attendance (Rensel et al., 2010). Likely because of the predictability of human-provided foods, suburban females are able to reduce the time spent away from the nest and increase their time brooding (Niederhauser & Bowman, in

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prep.), which may reduce nestling stress. Differences in baseline corticosterone may explain why suburban jays produce more UV-shifted plumage.

Alternatively, birds in our suburban population may, on average, have more UV-shifted plumage than wildland birds because the selection pressures (increased brood reduction and post-fledging mortality) in the suburbs are stronger. In the suburbs, few young survive to nutritional independence, whereas in the wildlands, mortality rates are lower and more individuals survive. However, because no relationship between color and condition is evident, this pattern cannot simply be a result of low quality individuals being culled from the suburban population. Assuming color is also related to dominance at our suburban site, dominant individuals may be out-competing their nest-mates for parental provisioning. Another possibility is that plumage elicits preferential provisioning from adults, similar to what is observed in eastern bluebirds (*Sialia sialis*) (Ligon and Hill, 2010). Either of these scenarios would result in duller nestlings being less likely to survive to independence.

We found that dominant birds were more likely to have higher mean brightness than subordinates at our wildland site, but not the suburban one. No relationship existed between dominance and UV chroma, or hue in either habitat. It is critical to note that these associations between dominance and color are not consistent across our studies. Data collected at Archbold Biological Station from 2008-2011 showed that dominant birds were no more likely to have higher mean brightness, UV chroma, or lower hue than expected by chance (Tringali and Bowman, 2012). However, using data only from 2008-2010, the result was different: dominant birds were significantly more likely to have the higher UV chroma than subordinates ($p = 0.01$, Probability of Success = 0.75, n = 24). These inconsistencies make interpreting the differences in binomial tests results between suburban and wildland habitats difficult. However, in wildland

juveniles an experimental treatment which reduced UV chroma and increased hue caused a reduction in dominance, which indicates that the UV component of plumage color is used in dominance signaling. Although the importance of mean brightness in status signaling is unclear, the experimental evidence that the UV component signals dominance among wildland juveniles is unequivocal (Tringali and Bowman, 2012). Experimental manipulations in the suburbs proved impossible because too few territories produced more than one young, which limited our ability to replicate experimental treatments.

In the absence of experimental data from the suburban population, we can consider two scenarios that assume that any signals are honest indicators of dominance: one in which honest signaling occurs in both habitats, and one in which honest signaling occurs in the wildlands and no signaling occurs in the suburbs. If plumage color honestly indicates dominance in both populations, then, on average, suburban birds should be dominant to those from the wildlands because they have more UV-shifted plumage. If this is the case, suburban birds that disperse to the wildlands have a good chance at out-competing the resident birds to obtain a breeding position. Under this scenario, the one-way dispersal from the suburbs to the wildlands would be facilitated. Suburban birds dispersing to the wildlands should be relatively high in the dominance hierarchy, and those that breed would likely realize higher nesting and fledging success and adult survival than in the suburban habitat (Breininger et al., 2009).

Likewise, wildland birds dispersing to a suburban area would have the opposite experience, possibly finding themselves lower in the dominance hierarchy and attempting to breed in a location with lower nesting and fledging success. If wildland individuals made pre-dispersal forays to the suburbs and encountered many challenges from local birds that perceived them as subordinate, thus potentially reducing their chances of acquiring a breeding territory,

they may not choose to settle in the suburbs. Although scrub-jays frequently disperse from our suburban population to the wildlands (38 settlers over approximately 18 years), over that same time period we recorded only a single bird from the wildlands settling in the suburbs. Of course, this pattern of one-way dispersal can also be explained by preference for high quality habitat.

If plumage color is an honest indicator of dominance in both habitats, but is only used as a signal in the wildlands, suburban birds dispersing to wildlands would still, on average, be more dominant than wildland birds. Wildland birds would perceive this difference, giving suburban birds a competitive advantage. However, this advantage would be countered by the suburban birds naiveté to the dominance signaling taking place in the wildlands. Suburban birds in wildland habitats may have a harder time navigating the dominance relationships of unfamiliar birds because they are "blind" to the plumage signaling. Status signals reduce the need to physically fight over resources, reducing the costs of social interaction. Individuals blind to these signals would have a higher cost of social interaction than those reading dominance signals. Because signals are useful in reducing the costs of social interactions, we think a scenario in which plumage color is an honest indicator of dominance, but is not used as a signal, would be unlikely.

We can also consider a scenario where, in the suburbs, plumage is not related to dominance and signaling does not occur. If this is the case, suburban birds are not likely to be, on average, more dominant than wildland birds. Suburban birds dispersing to the wildlands would not be more competitive than the wildland birds they encounter, and they wouldn't be privy to dominance signaling. In this scenario, cost of dispersal would be high, and the probability of breeding successfully would be low. We do not consider a case in which plumage is not a reliable indicator of dominance, but is used anyway, because this is unlikely (van Rhijn and

Vodegel 1980, but see Johnstone and Grafen 1993). Honesty of signals may be maintained by the cost incurred by cheaters (Számadó, 2011), in that subordinate birds with a dominant signal risk engaging in and subsequently losing interactions with dominant individuals more often (but see Gonzalez et al. 2002).

Unlike the example seen in cardinals, where the condition-dependence of color is relaxed in the suburbs, no relationship exists between Florida scrub-jay body condition and plumage coloration in either our suburban or wildland habitat. Because this relationship does not differ between habitats, there is little reason to believe the use of plumage signaling would differ. Assuming suburban birds are privy to plumage signals of dominance, we would expect them to be relatively successful in acquiring breeding positions after dispersing to the wildlands. This sets up an interesting dynamic where suburban-hatched birds that disperse to wildlands are likely to have higher reproductive success than those that remain in the suburbs to breed.

Although juveniles from our suburban site were in similar in size and body condition to those from our wildland site, and had more UV shifted plumage color, it is important to note that our suburban site is a sink (Breininger and Carter, 2003) and suffers from higher hatching failure (Aldredge, 2008), brood reduction (Shawkey et al., 2004), and post-fledging mortality (Bowman, 1998).While we found no evidence that the addition of anthropogenic food detrimentally effects status signaling, access to human provided foods is thought to explain why suburban birds feed inappropriate plant-based foods to nestlings (Sauter et al., 2006) and breed earlier than their wildland counterparts (Schoech, 1996). Currently, it is not known if the more UV shifted plumage of birds from our suburban site assists them in acquiring a breeding territory at our wildland site. For these reasons, we do not believe that the plumage differences we observed should be used to justify providing anthropogenic foods to Florida scrub-jays in suburban areas.

Plumage signals dominance in several species, and changes to dominance hierarchies can affect dispersal (Pasinelli & Walters 2002) and demography (Wong 2012). Changes associated with urbanization can affect both carotenoid-based (reds, yellows, oranges) and structural (greens, blues, UV) colors used in status signaling. These changes to plumage ornaments used for signaling may result in changes to social structure and metapopulation dynamics. Changes that reduce rates of reproduction or increase rates of dispersal in and around suburban sites should be of particular interest to conservation biologists and managers working in these areas.

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CHAPTER FIVE ~ CONCLUSIONS

Existence of sexually dimorphic ornamentation in juveniles is unusual. We typically think of sexual dimorphism as a product of sexual selection, either via female-choice or male-male competition. However, my research shows that sexually dimorphic juvenile color can evolve via social selection (Tringali & Bowman 2012). The relative importance of social dominance, male-male competition, and female choice in driving the evolution of sexual dimorphism will vary among species. Florida scrub-jays are highly social, socially and genetically monogamous, and typically breed very near their natal territory (Woolfenden & Fitzpatrick 1985). In a system such as this, where social relationships are formed early and may persist for the lifetimes of the individuals involved, establishing dominance early may have significant advantages. These benefits may be immediate, such as priority access to food, or deferred, such as increased likelihood to inherit or obtain a breeding territory.

A myriad of potential benefits to signaling dominant social status exist, and I found that mean brightness of both sexes and hue of females is significantly related to lifetime reproductive success. Although the deviance explained by these models was low, models incorporating adult color may significantly improve the fit. The correlation between adult and juvenile plumage is unknown, and to date, no studies on the function of adult Florida scrub-jay plumage coloration exist.

Although we do not know if juvenile plumage color predicts adult color, we can make a reasonable estimation based on what we know about the relative effects of additive genetic variance, and environmental and maternal effects. Both mean brightness and UV chroma are heritable, and although maternal effects were strong, environmental ones were not. Depending

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on how persistent maternal effects are, juvenile plumage color may be an excellent indicator of adult plumage.

Although my genetic model found very small environmental effects on plumage color, I found significant differences in plumage color between the suburban and wildland study sites. Surprisingly, suburban birds had more UV-shifted plumage, possibly because of access to limitless human-provided foods during the period of rapid feather development. Although I found no evidence that suburban birds use plumage to signal dominance status, this is likely a product of low power due to small sample sizes. Assuming plumage color is an honest indicator of dominance status in birds from both locations, these differences in UV-reflectance are likely to facilitate dispersal from the suburbs to the wildlands because suburban birds will be, on average, more competitive than wildland birds. This facilitated dispersal may be a factor in the rapid decline of suburban populations that is currently underappreciated.

My research represents some of the first evidence in juveniles for plumage signaling status and social selection driving the evolution of sexual dimorphism. Additionally, I am one of the first to describe differences in plumage color between individuals living in wild and urbanized habitats. My results are consistent with what is known about ornamental traits in adults, but suggest that the sexual-selection-centric view is a biased one. Studying juvenile ornamentation may provide insights into the evolution of sexual dimorphism, especially for highly social and sedentary species, such as the Florida scrub-jay.

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