BIRDS OF A FEATHER: INDICATORS OF QUALITY IN URBAN VERSUS RURAL EASTERN BLUEBIRDS (*SIALIA SIALIS*)

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ABSTRACT

BIRDS OF A FEATHER: INDICATORS OF QUALITY IN URBAN VERSUS RURAL EASTERN BLUEBIRDS (*SIALIA SIALIS*)

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Urban and rural populations of songbirds face different challenges in their habitats, including differences in predator types, food types and abundance, anthropogenic disturbances, and environmental cues such as temperature. These differences could affect individuals' body condition, including the investment they put into and speed at which they produce feathers. Feathers are an integral characteristic of bird anatomy and aid in functions such as flight, insulation, and display; they have been shown to vary in quality among populations. Using Eastern bluebird feathers collected from two urban and two rural sites, I measured the microstructure (barbule density), growth rate (growth bars), and weight/length of tail feathers to determine their quality. I also compared individuals' body weights and wing, tail, and tarsus lengths for urban versus rural populations and correlations with feather quality. I found positive correlations between the feather and body measurements, suggesting they both represent condition. There was a significant difference in the barbule density, tarsus length, and body weight across the four locations; however, the two urban sites had the best and worst conditions for these measurements. This suggests that urbanization could result in variable habitat qualities.

CHAPTER ONE: INTRODUCTION

Feathers are an integral characteristic of avian anatomy, serving in functions including flight, insulation, displays, and protection. Because of their many functions, the quality of feathers can directly impact the survival and reproductive success of individuals (Takaki, Eguchi, & Nagata 2001; DesRochers et al. 2009; Nilson & Svensson 1996; Dawson et al. 2000). For example, lower quality feathers can break and create gaps during feather growth, which affect birds' flight ability (DesRochers et al. 2009). Delaying feather growth, which often results in lower quality feathers, can decrease over-winter survival and reproductive success the following breeding season due to the birds having to expend more energy on thermoregulation (Nilsson and Svensson 1996). For birds with structural coloration, the composition and production of the feather can affect its brightness or hue, which can be honest signals in mate choice for reproduction (Siefferman & Hill 2003). With their importance in survival and reproduction, and the efforts put into their production, feathers can be used as indicators of an individual's condition in studying bird populations (Broggi et al. 2011).

Feather quality, including differences in feather weight and microstructure, is a variable trait among individuals and populations. Feather structure is comprised of a main rachis, with barbs that branch out from it, and barbules that branch from these barbs with hooklets to interlock with each other (Figure 1) (Lovette & Fitzpatrick 2016). All of these structures are made of keratin and grown from keratinocytes in the follicles of the bird's skin (Lovette & Fitzpatrick 2016). The complex of barbs and barbules is considered the feather's microstructure and is often used to determine the density of feathers as an indicator of quality (Figure 1). Denser feathers have more barbs/barbules, which suggests a higher allocation of resources was put into the feathers, and that they will be less likely to face breakage. Feather weight can also be used to infer density—feathers with more barbs and barbules packed into it would be heavier, and thus higher quality.

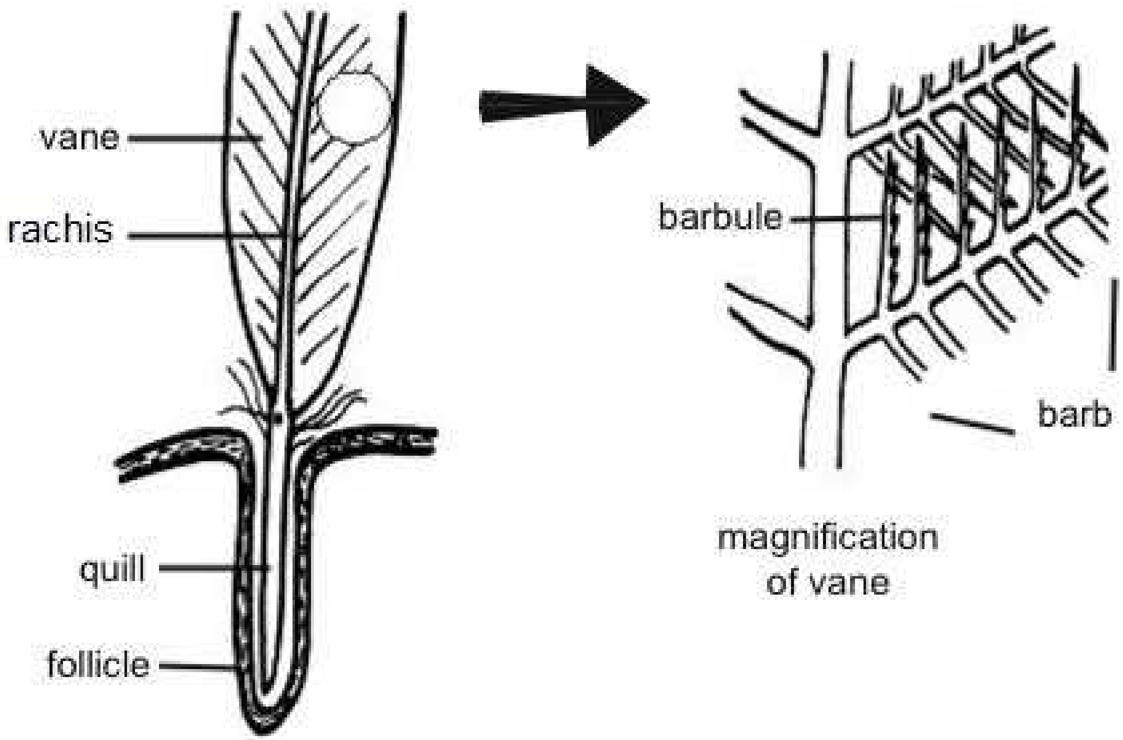

Figure 1. The anatomy of a feather, including the magnification showing the complex of barbs and barbules (see also Figure 3) (Connelly 2007).

Several studies have used feather weight and microstructure to look at variation between populations of birds. For example, there are differences in feather structure of Great tit (*Parus major*) populations from northern versus southern European sites, with the northern population having shorter, denser feathers (Broggi et al. 2011; Gamero et al. 2015). Similarly, species of sparrows restricted to mountain habitats have higher node density in plumaceous feathers when compared to more widely distributed sparrow species (Fu-Min Lei et al. 2002). The denser feathers of northern and mountain populations could be due to the thermoregulatory properties of feathers, with higher densities serving as better insulation. Migratory Blackcaps' (*Sylvia atricapilla*) rectrices were a lower mass than residential individuals, which shows the wear and tear that flight can have on feathers (Hera et al. 2010). Feather structure variation has been found within populations as well. In Japanese Jungle crows (*Corvus macrorhynchos*), males have a higher density of barbules and shorter inter-barbule distances than the females; this may have an effect on their color, which could explain the pressure for males to have higher quality feathers (Lee et al. 2009). A positive correlation of barb count and nestling period duration was found in juvenile feathers of several Passerine species, suggesting a trade-off between feather quality and body development (Butler et al 2008). Overall, feather measurements serve as a reliable means to determine differences in the condition of birds facing different external challenges.

In addition to measurements such as microstructure, feather growth can also be used to infer differences in their quality. Feather quality is often a result of the speed at which the feather is grown during the molting period. Molting is an annual process in birds where old, worn feathers are shed and new feathers grow in their place (Lovette & Fitzpatrick, 2016). A field study of urban versus rural chickadees' (*Poecile carolinensis*) molt found that although the onset of molt was earlier in the urban population, the duration was about the same, and the intensity of the molt was much lower in urban areas (Hope et al. 2016). Urban birds grew in fewer feathers simultaneously than birds in natural areas. This must mean that the urban chickadees grow individual feathers quicker than rural birds, and they could be sacrificing feather quality to do so (Hope et al 2016). Experimentally manipulating the molting period of birds results in lower quality feathers that grow in quickly after the breeding season, whereas birds that molted slowly have better quality feathers, determined by their heavier weight (Nilsson and Svensson 1996; Dawson et al. 2000).

Rather than molt, other studies have used growth bars, which are light and dark bands on the feather that indicate nightly and daily growth, to measure feather production rates. Birds with wider bands means more of the feather grew within a day. Contradictory to the molt study, growth bar studies suggest birds with wider bands have better nutritional status, can allocate more resources to growth, and therefore produce higher quality feathers (Takaki et al., 2001; Grub, 1989).

While there have been studies on feather quality in regards to environmental differences such as geographical location, only a few have looked into the influence of urban versus rural habitat. In addition to Hope et al.'s (2016) study of molt previously mentioned, a study of house sparrows (*Passer domesticus*) in urban versus rural sites looked at feather quality (mass:length ratio) and body size of both juveniles and adults to determine the effect of urbanization on birds during different life stages (Meillere et al. 2017). For adults, there was no difference in feather quality across the urbanization gradient, but juveniles had worse feather quality with increasing urbanization, and both adults and juveniles were smaller in the more urban sites. Adult house sparrows are able to sustain their feather and body condition, but urbanization creates a more stressful environment and a nutritional deficit for younger birds (Meillere et al. 2017). Similarly, a study of body size, plumage coloration, and telomere length in Great tit nestlings in urban versus rural habitats found that the rural chicks were heavier and had more colorful plumage (Biard et al 2017). However, the Great tit nestlings' plumage is due to carotenoid deposits, and thus may not be reflective of the feathers' structural quality.

Populations of songbirds in urban areas face different challenges than those in natural or rural settings, including changes in predation, food availability, habitat structure, environmental cues such as temperature, and anthropomorphic disturbances such as noise, light, and chemical pollution (Chamberlain et al. 2009; Hope et al. 2016; Meillere et al. 2017; Biard et al. 2017; Jackson et al. 2011; Kight et al. 2012; Isaksson & Andersson 2007; Liker et al. 2008; Bonnington et al. 2015). For example, while manicured, urban habitats may attract adult birds, they can have a detrimental effect on the survival of fledglings due to habitat structure that causes the birds to be more exposed to predators (Jackson et al. 2011 & 2013). Similarly, the abundance of urban dwelling predators such as corvids and grey squirrels could harm the reproductive output of songbirds (Bonnington et al. 2015).

For feather production and quality, the differences in food availability of urban and rural habitats could be especially influential. Feather production requires a high allocation of protein, so restriction in diet could put a strain on such demands (DesRochers et al. 2009). Food restricted birds have lower quality feathers that are more prone to breakage (DesRochers et al. 2009). Similarly, Zebra finches (*Taeniopygia guttata*) with unpredictable food supply had lower barbule density and longer inter-barbule distances (D'Alba et al 2014). Younger urban birds have lower quality or duller colored feathers because food readily available to birds in urban sites may suffice for adults but lack in nutrition for the high demands of a growing individual (Meillere et al. 2017; Biard et al. 2017). While human-provided food, such as bird feeders, could improve adult body condition, it has been found that nestlings face starvation and have lower body weights because the type of food available is not suitable for nestlings' diet (Chamberlain et al. 2009). When both are available, birds show a preference for natural foods over human-provided food that is common in urban areas (Chamberlain et al. 2009). In regards to the natural foods available in urban areas, a study on the primary diet of Great tits—caterpillars—found that while urban sites had a higher abundance of caterpillars, the caterpillars were lower quality with regard to their carotenoid concentration (Isaksson and Andersson 2007).

The differing types or quality of food available for urban versus rural birds could influence the allocation of energy and protein to feather production. Other ecological factors could also influence the differences in feather quality. For instance, if urban birds live more sedentary lives than rural birds, their demands for feather quality may not be as high as birds in other habitats because they will face less wear and tear over time. Research sites could have differences in predation risk that could play a more influential role in the birds' body condition than urbanization itself (Meillere et al. 2017; Biard et al. 2017). The differences of body size and feather quality in urban areas could be either a constraint or an adaptive trait (Meillere et al. 2017). Often in the case of urbanization, the constraint hypothesis is more commonly used to explain differences, implying that urbanized areas are the less preferred habitat for birds, but it is worthwhile to acknowledge that urban sites are not necessarily always worse.

While a few studies have been done on feather quality of urban versus rural birds, they only focused on a single measurement of feather quality each—coloration in Biard et al. (2017), and feather mass/length in Meillere (2017), molt in Hope et al. (2016). They also were done on house sparrows and Great tits, species that are considered urban dwellers, which can thrive in these areas despite the decline in diversity that is usually associated with urbanization (Chamberlain et al. 2009).

My study subject, Eastern bluebirds (*Sialia sialis*), are an insectivorous, cavity nesting species that is often considered a conservation success due to nest boxes placed in urban, managed landscapes such as parks and golf courses (Jackson et al. 2013). Because of this, they have been a study species for urban versus rural habitat for aspects such as fledging survival (Jackson et al. 2011 & 2013), as well as in many studies of feather coloration as an honest signal in mate choice (Siefferman and Hill 2003 & 2007). My research uses a collection of Eastern bluebird feathers from four sites, two urban and two rural. In this collection, I studied feather quality in multiple measurements, including microstructure, growth, weight, and length. In addition to the feathers, body condition measurements were taken of the birds at the time of collection, which included body weight and wing, tarsus, and tail length.

I expected to find a difference in the feather quality and body condition of bluebirds from the urban and rural populations. Due to the insectivorous diet of the species, I expected that the birds may be constrained in urban areas, which would be reflected in their body size and/or feather quality. I also expected to find positive correlations between the feather and body measurements, indicating that they both represent condition of individuals.

CHAPTER TWO: METHODS

Feather Collection

The Eastern bluebird feathers used in this study were collected in 2013 from nest boxes located in Carroll County, Georgia (33°58’ N, 85°08’W) (Figure 2) (Graham 2014). Two sites, Campus and Town, were designated as urban, mostly consisting of lawns close to homes, buildings, and parking lots (Graham 2014). The other two, Farm and Lowell, were designated as rural, located at the edge of agricultural farms that were lined by wooded areas (Graham 2014). Two rectrices were collected from each bird, as well as several contour feathers from the breast and back. During the collection process, several condition measurements were taken, including body weight, and wings, tail, and tarsus lengths (B. Ballentine, unpublished data). These feathers were stored in envelopes and kept in a refrigerator to maintain their quality. For my analyses, I used the right rectrix of each bird and a back contour feather, and my sampling included 62 individuals: 22 Campus, 10 Town, 17 Farm, and 13 Lowell; 31 males and 31 females.

Figure 2. A map of the nestbox locations, taken from Graham (2014). In legend, “lakecarroll” is labelled Town site in my research, “cowfarm” is Lowell, “hayfarm” is Farm, and “campus” is the same.

Microscopy

I used an EVOS digital microscope to take pictures of the feathers’ microstructure. Images were acquired in brightfield mode using a 20x objective. The pictures consisted of a portion of the barb and the barbules attached. I created an apparatus consisting of 2 microscope slides, a ruler, and a piece of cardstock to hold the feather when using the microscope that would ensure that the same area of each feather was taken for the image (Figure 3).

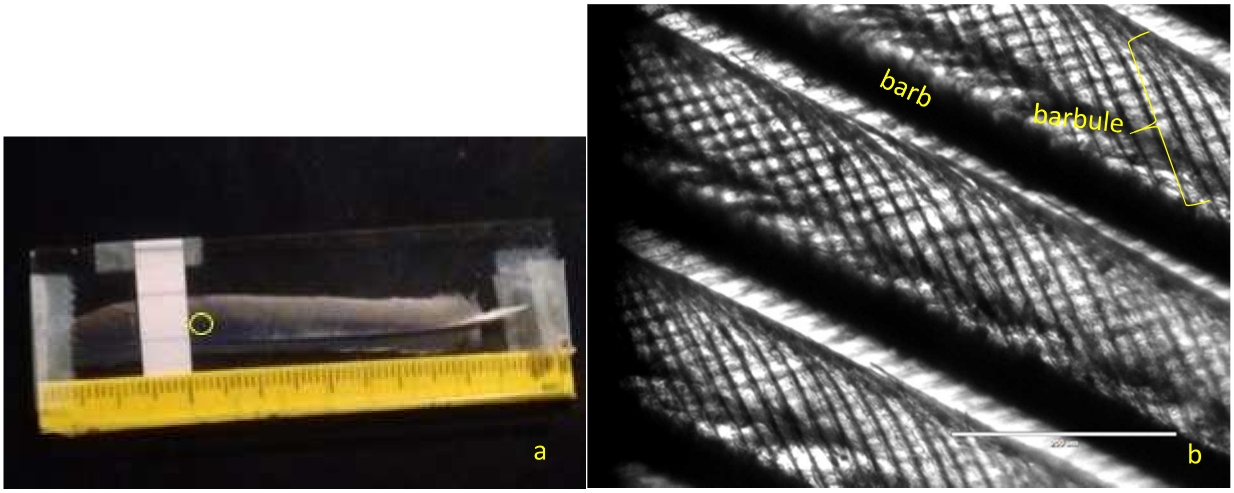

Figure 3. A bluebird rectrix in the slide appartus, cardstock at 50 mm mark on ruler (a), with the indication of the part of the feather that the photo of the microstructure was taken (b), with a scale bar of 200 µm.

Tail feathers. I wanted to make sure to take images of the same area on each feather, the upper mid-inner vane section. In order to account for length, I would take the image at the 50 mm mark on the ruler attached to the slide (Figure 3).

To account for the width of the inner vane, I scanned the feather to find the rachis, which was easily recognized because it was much thicker than the barbs. From the rachis, I would then scan up into the inner vane, and I would take the image of the fifth barb up from the rachis. This way I was taking the picture in the middle of the vane—not too close to the edge that could have faced more wear and tear, nor too close to the rachis.

Body feathers. For the contour back feathers, the two-slide apparatus was still used to hold the feather in place, but the ruler and vertical marker were unable to be used because of their smaller sizer. Body feathers consist of both pennaceous and plumaceous sections, so for these feathers I took two pictures, one of one each part. Since each section of the feather was so small, I was less concerned about picking a consistent area on each feather, and instead took images of what I could get a clear focus on.

Microstructure Measurements

Once the pictures were taken of all the feathers, I used ImageJ to take the measurements of their structure. The image that the EVOS microscope took included a scale bar at the bottom of the picture, and I used this to set a global scale of micrometers for measurements. For both the tail and the pennaceous section of the body feathers, I measured barbule density. For the plumaceous section of the body feathers, I measured average internode distance.

Barbule Density. Barbule density was calculated by first measuring 0.5 mm of the barb's length by using the global scale feature. Using ROI Manager feature in ImageJ, I then counted the number of barbules that were on this barb for the length of 0.5 mm.

Internode Distance. For the plumaceous portion of the body feathers, I took images that focused on the nodes of feathers. I measured the length between two nodes to account for their distance. I measured the internode distance three times in each picture and took the average of the three measurements.

Feather Growth Bars, Length, and Weight

In addition to the microstructure of the feather, I also took other common measurements of the tail feathers, including the feather weight and their growth bars. I weighed each right rectrix using a digital balance and recorded their weight to the nearest thousandth of a gram. For the growth bars, I also used the right tail feather, and I created a modified version of Grub's (1989) method for measuring them.

I taped each feather onto a piece of black cardstock, which was pinned down to Styrofoam. I would first pin the tip of the rachis and the very end of the feather in order to determine the overall length. Then, working in a darkroom with a small desk lamp as the only light source directly above the feather, I could visualize the growth bars, and would use a pin to stick through each dark band of the inner vane, adjacent to the rachis. I pinned as many as I could see distinctly on the feather, with most being in the center of its length rather than near the ends of the feather. This resulted in the cardstock having holes that represented the length of the feather and its growth bars.

Using calipers, I first measured the length of the feather with the two end holes. Then using its length, and following Grubb (1989), I calculated the two-thirds point in the length of the feather and used calipers to determine the growth bar mark that was closest to this point. Grubb (1989) measured and averaged the length of 10 growth bars, 4 above and 5 below the two-thirds growth bar point. However, bluebird tail feathers are small, and I would often only get ten or so growth bar points in total, including the outlier ones at the very ends that could skew the data. Instead of averaging 10 growth bars, I measured six, three above and three below the two-thirds point, and then calculated the average growth bar length of these six measurements.

Statistical Analysis

I used R Studio and Microsoft Excel to conduct all of my analyses. For comparisons, such as between urban and rural, the four locations, or males and females, I ran ANOVAs for all the measurements. I also used Tukey's honestly significant difference (HSD) *post hoc* tests for comparisons between sites. I used Pearson's coefficient to determine any correlations between measurements.

CHAPTER THREE: RESULTS

Microstructure Measurements

Tail feather barbule densities averaged 18.77 barbules per 0.5 mm, ranging from 17-23 barbules. Body feather barbule densities averaged 14.25 barbules per 0.5 mm, ranging from 11-17 barbules. There were no significant differences in urban versus rural or between the sexes for any of the microstructure measurements (Table 1). However, there was a significant difference in barbule density of the tail feathers among the four sites (Figure 4). Rather than urban or rural sites having greater density, the two urban sites had the highest and lowest densities; campus had the highest and town had the lowest, while the two rural sites were at intermediate levels (ANOVA, F_3= 3.15, p = 0.032) (Table 1). The Tukey's *post hoc* test confirmed that the differences between the two urban sites were significant (campus vs town, Tukey's HSD test, p = 0.019).

Table 1. F and p values of ANOVAs of feather and body measurements for comparisons of urban versus rural, among the four sites, and between sexes.

	Urban vs Rural	Among Four sites	Male vs Female
Rectrix barbule density (# barbule per 0.5mm barb)	F_3= 0.027 p = 0.871	F_3= 3.15 p = 0.032*	F_3= 0.179 p = 0.674
Rectrix mass/length (g/mm)	F_3= 0.204 p = 0.653	F_3= 0.142 p = 0.935	F_3= 15.62 p = 0.00021***
Contour barbule density (# barbule per 0.5mm barb)	F_3= 0.639 p = 0.427	F_3= 1.07 p = 0.369	F_3= 0.028 p = 0.867
Contour internode distance (µm)	F_3= 0.021 p = 0.886	F_3= 0.484 p = 0.694	F_3= 0.107 p = 0.745
Growth bars (mm)	F_3= 0.354 p = 0.554	F_3= 0.187 p = 0.905	F_3= 0.407 p = 0.526
Body weight (g)	F_3= 0.385 p = 0.537	F_3= 3.442 p = 0.023*	F_3= 0.212 p = 0.647
Wing Length (mm)	F_3= 3.06 p = 0.085	F_3= 2.337 p = 0.083	F_3= 8.029 p = 0.00626**
Tarsus length (mm)	F_3= 0.259 p = 0.612	F_3= 3.018 p = 0.037*	F_3= 0.003 p = 0.958

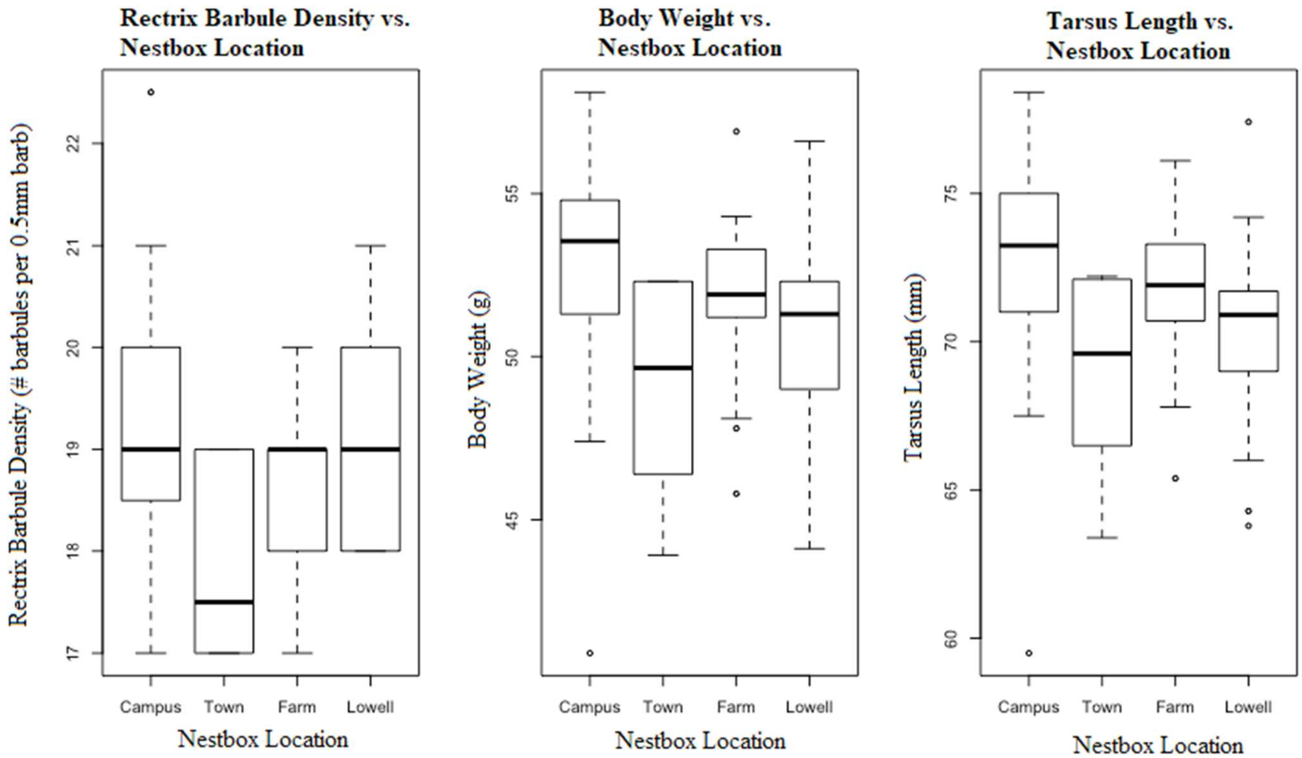

Figure 4. Significant differences among the four nest box sites with comparisons rectrix barbule density, body weight, and tarsus length (ANOVAs, see Table 1). Error bars are standard deviation, circles represent outliers and the median and quartiles are shown.

Feather Growth Bars, Length, and Weight

Growth bars averaged 2.81 mm, ranging from 2.2-3.967 mm. There were no significant differences in any of the comparisons for growth bars (Table 1). The average length of tail feathers was 67.1 mm (range 62.1-74) and the average weight was 0.0143 g (range 0.012-0.0172). For length and weight of the tail feathers, there was no difference for urban versus rural or the four sites, but there was a difference between males and females (ANOVA, F_1=15.62, p= 0.0002), with males having longer, heavier feathers than females (Table 1; Figure 5).

Body Measurements

The average body weight was 51.45 g, average wing length was 96.24 mm, tarsus length was 18.845 mm, and tail length was 61.166 mm. When accounting for body weight, wing length followed a similar pattern to the feather length and weight, with only a difference between the sexes, males having the longer wings (ANOVA, F_1= 8.029, p= 0.007) (Table 1; Figure 5).

On the other hand, body weight followed a similar pattern to the tail barbule density, showing a difference among the four site locations, with the heaviest birds at the campus site and the lightest weight at the town site (ANOVA, F_3= 3.442, p= 0.023) (Table 1; Figure 4). The difference between the two urban sites was confirmed (campus vs town, Tukey's HSD test, p = 0.027). Additionally, tarsus length, once body weight was accounted for, followed the same pattern (ANOVA, F_3= 3.018 p = 0.037), and the difference between the two urban sites was confirmed (campus vs town, Tukey's HSD test, p = 0.043) (Table 1; Figure 4). This pattern also repeated itself when comparing males only among the four sites for body weight (ANOVA, F_3= 3.827, p= 0.021) and tarsus length (ANOVA, F_3= 3.407, p= 0.0318).

Figure 5. Significant differences between sexes in comparisons of rectrix mass/length and wing lengths (ANOVAs, see Table 1). Error bars are standard deviation, circles represent outliers, and median and quartiles are shown.

Correlations

In comparing feather measurements with typical body condition measurements, Pearson correlations show that the rectrix mass/length positively correlates with all three body measurements, and tail feather barbule density positively correlates with body weight and tarsus length (Table 2). Wing and tarsus lengths also have a significantly positive correlation (Table 2).

Table 2. Pearson (r) correlations of all feather and body measurements of Eastern bluebirds

	Rectrix mass/length	Contour barbule density	Contour internode distance	Growth bars	Body weight	Wing length	Tarsus length
Rectrix barbule density	0.198	0.179	-0.146	-0.08	0.338**	0.028	0.251*
Rectrix mass/length		0.0768	-0.126	0.157	0.277*	0.314*	0.332**
Contour barbule density			0.031	0.141	0.016	0.138	0.096
Contour internode distance				0.086	-0.187	-0.024	-0.126
Growth bars					0.17	0.01	0.034
Body weight						0.116	0.197
Wing Length							0.251*

*P<0.05, **P<0.01, ***P<0.001

CHAPTER FOUR: DISCUSSION

I studied the feather quality and body condition of Eastern bluebirds from two urban and two rural sites. I found positive correlations of rectrix weight/length and barbule density to the body measurements, which show that rectrices can be used to determine quality of individuals. The body measurements in these correlations are widely used to interpret individuals' condition, and with the feather measurements significantly correlating with them, this reinforces that feather microstructure and weight can be used as condition measurements as well.

Conversely, I found no correlations between growth bars and measurements of body condition, suggesting that growth bars are not informative feather measurements. Originally thought to represent nutritional status, growth bars represent a 24-hour period of growth, and as suggested in more recent studies, the speed of feather production does not correlate with quality (Hope et al. 2016; Dawson et al. 2000). There were also no significant correlations with contour feather microstructure and body measurements.

I found that at all sites, males and females did not differ in feather microstructure, but males had longer, heavier feathers, as well as longer wings than the females (Figure 5). Since Eastern bluebirds are sexually dimorphic, perhaps it is intuitive that the males would have larger wings with longer feathers. Due to the pressures of sexual selection, males' feathers have been shown to indicate quality as an honest signal in obtaining mates and the males' parental care involvement (Sifferman and Hill, 2003). Longer, heavier rectrices and larger wings, as found in my study, could enhance in flight ability and survival, which the females could find attractive during mate selection, since better fliers could catch food more easily and aid better in raising offspring. Males could be under pressure to grow larger flight feathers for survival and reproductive success.

My research indicates that there was no overall difference in feather quality or body condition in urban versus rural bluebird populations; rather, some urban sites were more favorable than others, whereas rural sites were more consistent. This was reflected specifically in barbule density, body weight, and tarsus length (Figure 4). Body weight and tarsus length differed among sites in males as well. The campus urban site had the heaviest birds with the largest tarsi and the densest rectrices, whereas the town urban site had the lightest weight, smallest birds with the least dense rectrices. Both rural sites had similar, intermediate body weights, tarsi lengths, and barbule densities.

The differences in body weight, tarsus length, and rectrix barbule density measurements between the two urban sites suggests that the two sites may represent very different quality habitats. The town site was described as having nest boxes near roads in a more suburban, neighborhood setting. This could differ from the nest boxes set up on a university campus, where there could be more foot traffic as opposed to vehicles on roads. It is possible that the town site was an ecological trap, where it had the appearance and appeal of a more rural site, but in reality, these birds had to face more disturbances, namely anthropogenic noise and pollution via cars, or changes in the types or abundance of predators. In a study of European blackbirds (*Turdus merula*), urban sites were ecological traps, because the songbirds did not alter their nesting locations or clutch sizes despite the higher abundance of corvid and grey squirrel predators, which could have a negative effect on the songbirds' reproductive success (Bonnington et al. 2015). Eastern bluebirds in areas of high anthropogenic noise had smaller brood sizes and reduced productivity (Kight et al. 2012). At the individual level, house sparrows had smaller body sizes in more urbanized areas (Liker et al. 2008). Similarly, in my research, bluebirds at the town site were in poorer condition than those at the other sites, suggesting that they were facing some of the negative effects of urbanization, perhaps despite an initial appeal that drew them to nest there.

While the campus site likely had anthropogenic disturbances as well, perhaps they were less threatening disturbances. For example, birds in urban areas tend to have shorter flight initiation distance since they perceive humans as non-threatening (Moller 2008; Lin et al. 2012). Specifically, in Eastern bluebirds, urban males were more aggressive in playback experiments; aggressive tendencies have been found to correlate with boldness, which could be favorable in more human populated areas (Graham 2014). The campus birds were not negatively affected by urbanization, suggesting that the disturbances of this site were not ones that put them under stress and lessened their overall body condition.

While the town site may have been an ecological trap, with birds showing poorer condition, the campus urban site had the birds in best condition, indicating that not all urban sites should necessarily be assumed as the worst habitat. There have often been contradictory findings when looking at condition or reproductive success in urbanization studies, in some cases finding that birds in urbanized areas can thrive (Chamberlain et al. 2009). For instance, Northern cardinals (*Cardinalis cardinalis*) were more abundant in urban areas and had equally successful reproductive output as their rural counterparts (Leston and Rodewald 2006). Similarly, urban Great tits had on average one more fledging than rural birds, implying that urban birds had greater reproductive success (Isaksson and Andersson 2007).

Urban habitats can vary greatly based on the geography and landscape of the sites used (Liker et al. 2008; Chamberlain et al. 2009). “Urban” is rarely quantitatively defined, and urbanization studies include any landscape involving buildings, ranging from commercial and industrial areas to more suburban, residential areas, or include green spaces such as parks within a city (Chamberlain et al. 2009). In a study of house sparrow body size, urbanization based on land cover (buildings, roads, vegetation) accounted for urbanization more than human utilization of those sites or distance from the city's center (Liker et al. 2008). In another instance, a study of urban and rural populations of Great tits found that urban nestlings were smaller, but this difference was only true for the most urbanized populations (Biard et al. 2017). Variation in urbanization could explain the potential of some urban sites being truly high quality whereas others could be ecological traps. In the case of my research, it seems that the campus site was high quality habitat, as reflected in the denser feathers and larger body sizes, whereas the town site birds were in poor condition.

Another possible explanation in the differences between the sites could be the diet available to the bluebirds in each habitat. Food availability is a huge influence on feather growth and production, as well as body weight, so it is possible that the suburban habitat of the town site was lacking in resources compared to the campus and rural sites. Bluebirds are mainly insectivorous, so perhaps the town site was lacking in insect abundance, or the insects themselves were of lower quality in that area, such as Isaksson and Andersson (2007) found in their study. Lower quality feathers and smaller size of urban juvenile birds are likely because the food available to them was lacking in nutritional resources for the demands of their age (Meillere et al 2017; Biard et al. 2017; Liker et al. 2008). One of the most prevalent issues in urban habitats is the lower quality food, which is most costly to developing birds (Chamberlain et al. 2009). Perhaps the bluebirds at the town site faced these constraints during development and never fully recovered from it, resulting in small body size as adults.

An explanation for the similar conditions among the sites, such as wing lengths of the bluebirds, as well as the individuals having high condition in one urban site, could be the species of the study. No matter the site, the bluebirds' general habitat remained the same—bluebirds are cavity nesters that prefer edge habitat. No matter whether the edge was in an urban or rural environment, the immediate vicinity of the bluebirds from the collection lived in nest boxes that were posted in appealing, edge habitat. In a study of species distributions across an urbanization gradient, insectivorous and cavity nesting species were able to survive in higher degrees of urbanization than most other species (Sorace and Gustin 2010). Bluebirds are both insectivorous and cavity nesters, so perhaps due to the species' ecological preferences, the level of anthropogenic disturbances had less effect than it would have on a more sensitive species with different diet or habitat preferences.

Feather growth is a demanding process that requires allocation of resources and energy to produce high quality feathers. If birds are facing other pressures, they may give up higher quality feathers in favor of something else, such as immune responses (Isaksson and Andersson 2007; Ben-Hamo et al. 2017). For example, when house sparrows had their feathers plucked and were then given an injection to initiate an immune response, new feathers grown were poorer quality (Ben-Hamo et al. 2017). While sometimes necessary, sacrificing feather quality remains detrimental to a bird's condition, considering that feathers are important to survival in flight and thermoregulation, as well as reproduction success via displays and to serve as honest signaling to potential mates (DesRochers et al. 2009; Nilson & Svensson 1996). Because of this, feathers can serve as an indicator of condition along with more common measurements such as body weight and tarsus length, which is reflected in my own research (Figure 4).

I found that Eastern bluebirds' feather and body condition were not strongly impacted by urbanization, but rather that one urban site appeared to be high quality habitat, while another urban site appeared to be low quality habitat. The birds in this study were all from nest boxes in urban and rural sites. Rectrix barbule density, tarsus length, and body weight showed differences among the four sites. Future studies could integrate more sites and differentiate between urban and suburban habitats, as well as take into consideration differences among the edge habitat where the nest boxes are to better determine the pressures each population is facing that could impact their condition.

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