Sex-specific relationships between urbanization, parasitism, and plumage coloration in house finches

Brooke E. SYKES§, Pierce HUTTON, and Kevin J. McGRAW*

School of Life Sciences, Arizona State University, Tempe, AZ 85287

*Address correspondence to Kevin J. McGraw. E-mail: kjmcgraw@asu.edu

§Current address: Department of Biology, University of Mississippi, Oxford, MS 38677

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Abstract

Historically, studies of condition-dependent signals in animals have been male-centric, but recent work suggests that female ornaments can also communicate individual quality (e.g., disease state, fecundity). There also has been a surge of interest in how urbanization alters signaling traits, but we know little about if and how cities affect signal expression in female animals. We measured carotenoid-based plumage coloration and coccidian (Isospora spp.) parasite burden in desert and city populations of house finches Haemorhous mexicanus to examine links between urbanization, health state, and feather pigmentation in males and females. In earlier work, we showed that male house finches are less colorful and more parasitized in the city, and we again detected such patterns in this study for males; however, urban females were less colorful, but not more parasitized, than rural females. Moreover, contrary to rural populations, we found that urban birds (regardless of sex) with larger patches of carotenoid coloration were also more heavily infected with coccidia. These results show that urban environments can disrupt condition-dependent color expression and highlight the need for more studies on how cities affect disease and signaling traits in both male and female animals.

Key words: carotenoid pigmentation, female ornaments, Haemorhous mexicanus, parasites, urban ecology

Honest signaling theory posits that elaborate sexual signals like songs, courtship dances, horns, or colors are differentially costly among signal bearers and therefore serve as condition-dependent indicators of quality (Andersson 1994; Johnstone 1995). Due to competitions for access to female mates and for valuable reproductive resources (e.g. territories), males of many species tend to show greater expression of these traits, and thus the majority of studies on condition-dependent signals have been done on males (Badyaev and Duckworth 2003). However, in several animal species, females also express forms of sexual ornamentation. Some elaborate female traits can be explained by correlated trait responses to sexual selection on males (Clutton-Brock 2009), but in several other systems female ornamentation, like in males, can also be linked to individual or environmental quality (Jawor et al. 2004; Martinez-Padilla et al. 2011; Osmond et al. 2013) and fitness (Roulin et al. 2001; López-Rull et al. 2007; Doutrelant et al. 2020). In such instances, there is also
evidence for male mate choice based on the quality of a female ornament (Hill 1993a; Amundsen et al. 1997; Amunden and Forsgren 2001) as well as female-female competitive interactions that are mediated by signals (Midamegbe et al. 2011).

In the past two decades, there has been a surge of interest in studying how rapid environmental perturbations, including anthropogenic shifts like urbanization and climate change, affect animal signals (Hill 1995; Hutton and McGraw 2016; Delhey and Peters 2016). Urban development in particular has served as an ideal point-source for tracking how human population growth and activities in cities affect animal condition as well as expression of indicator traits (Marzluff 2001; Shochat et al. 2006; Lizee et al. 2011). Many environmentally sensitive traits in animals, including hormones (Fokidis et al. 2009; Bonier 2012; Dominoni et al. 2013), antioxidant levels (Møller et al. 2010; Giraudeau and McGraw 2014), immunity (Bailly et al. 2016), disease (Giraudeau et al. 2014), behavior (Blumstein et al. 2005), and reproductive phenology (Davies and Deviche 2014) are known to be affected by urbanization. Thus, it is not surprising that urban activities can disrupt expression of condition-dependent animal signals including bird song (Mendes et al. 2011) and coloration (e.g. Jones et al. 2010; Hasegawa et al. 2014).

House finches *Haemorhous mexicanus* have served as a good model for studying urban impacts on ornamental traits. Males display prominent sexually selected red, orange, and yellow carotenoid-based plumage coloration (i.e. on the crown, breast, and rump; Hill, 2002), but some females also display hints of such color on their rump (and even more rarely on their crown and breast; Badyaev et al. 2020). These carotenoid colors in birds are sensitive to many environmental factors, including nutrition (Hill 2000), health (Saks et al. 2003), and urbanization (Biard et al. 2017, Sumasgutner et al. 2018). We have previously shown in our study population in and around Phoenix, Arizona, USA that urban males are less colorful than rural males (Hasegawa et al. 2014, Giraudeau et al. 2015); the same has been found for the carotenoid-based colors of male northern cardinals (*Cardinalis cardinalis*; Jones et al. 2010) and great tits (*Parus major*; Isaksson et al. 2005). However, it is not clear whether urbanization affects female plumage color in the same direction or magnitude. We also know that parasite load is an important driver of carotenoid coloration in male house finches (Thompson et al. 1997; Brawner et al. 2000; Hill et al. 2004) and other birds (Hőrak et al. 2004; Baeta et al. 2008). In prior work, we found that urban male house finches were more heavily parasitized by an intestinal protozoan coccidian (*Isospora* spp.) than rural males (Giraudeau et al. 2014; also see Delgado-Velez and French 2015 for a similar result in red-browed finches, *Neochmia temporalis*). This raises the question of whether, as in males, female parasite burden is linked to both urbanization and coloration. To date, we have learned that plumage color variation in female house finches is age-dependent, such that younger females are redder than older females (Hill 1993b), and that, in laboratory mate-choice tests, redder females are preferred as mates (Hill 1993a), though in the field males pair with older, more experienced females (who tend to have yellow or absent carotenoid coloration). However, unlike studies on males of this species, nothing is known of disease- or urban-dependent color expression in females.

Thus we aimed to examine relationships between parasite burden, plumage color expression, and urbanization in female house finches and to compare these to patterns observed in male house finches of the same populations. Specifically, we sought to determine if urbanization similarly affects disease status and plumage coloration in both sexes, and if the relationship between coloration and disease differs between sexes in urban versus rural populations. We measured ornamental plumage coloration, body condition, and coccidial...
parasite loads of wild male and female house finches captured from both rural and urban habitats. We predicted that, as in males, females would be less colorful and more parasitized in the city, and that redder males and females would be less parasitized by coccidians. However, if sexual selection acts more intensely on male ornaments, then the relationship between color and health may be more pronounced in males than females. It is also possible that, because of different age-related patterns of color expression for the two sexes, the urban environment differently impacts male and female coloration or parasitism.

Materials and Methods

Field Methods

From 17 October – 4 November 2015 (just after pre-basic moult; McGraw and Hill 2004), we captured a total of 95 ($n = 45$ female and $n = 50$ male) house finches from four different sites in the Phoenix metropolitan area: two urban (Arizona State University (ASU) - Tempe campus, downtown Phoenix residence) and two rural (Estrella Mountain and South Mountain regional parks), which differ significantly in both land-use/land-cover metrics and human population density (see Giraudeau et al. 2014 for additional site details). We maintained wire feeders with black oil sunflower seeds for one week prior to trapping, and birds were captured using basket traps hung around feeders. At capture, each bird was banded with a numbered United States Geological Survey tag for identification and examined visually (by P.H. and B.S.) to determine sex based on plumage coloration (Hill 2002). We could not determine age of these birds at this time of year because all finches were in adult plumage.

Body mass was determined to the nearest 0.1 g using a digital scale (Smart Weigh, Chestnut Ridge, NY), and tarsal bone length was measured to the nearest 0.1 mm using digital calipers (Neiko Tools, Homewood, IL) so that we could also evaluate body condition as the residuals saved from a linear regression between tarsus length and body mass ($F_{1,93} = 10.15, P = 0.002$; sensu Toomey and McGraw 2009; Burtka and Grindstaff 2014; Trigo and Mota 2014). Birds were inspected visually (by P.H. and B.S.) and scored for poxvirus infections, but poxvirus prevalence was very low in this study ($n = 3$ birds), so pox infection prevalence and severity were not included in further analyses. All birds were processed at the ASU-Tempe campus and photographed to obtain color metrics. Photos were taken with a Sony Cyber-Shot DSC-W800 in a dark room and with consistent flash settings, subject distance, camera presets, and background (grayscale photography card; Hasegawa et al. 2014). Each plumage patch of carotenoid coloration (crown, breast, and rump in males; same patches in females when red/orange/yellow color was present there) was photographed twice, and images were analyzed in Adobe Photoshop CS6 (Adobe Systems, San Jose CA, USA). We selected carotenoid color patches using the quick selection tool in Photoshop and obtained patch size (in pixels) and RGB values using the Histogram window (Giraudeau et al. 2013). Hue, saturation, and brightness values were computed from corresponding RGB values using the ‘Color Picker’ function. A size standard (of known area) was included in each photograph in order to convert number of pixels to mm$^2$. Females that lacked visible patches of red/orange/yellow plumage pigmentation were not photographed or analyzed for hue, saturation, and brightness.

Quantification of coccidian endoparasitism

After being photographed, birds were individually housed in small cages with ad libitum access to seed and water within an indoor vivarium on the ASU-Tempe campus. Due to the diel shedding cycle of coccidian
gametes (i.e. in the late afternoon and early evening; Brawner et al. 2000), we housed finches until 1630 hrs., at which point we changed the paper in each bird’s housing cage and returned to the housing room at 1730 hrs. to scrape small (ca. 0.25 g) fecal samples from the cage paper into 1.5 ml screw-cap Eppendorf tubes containing 1 ml of 2.2% potassium dichromate. Samples were stored in the dark at room temperature until analysis (1–2 months later). We measured presence and severity of coccidian infection using standard fecal-float and microscope-slide preparations (Brawner and Hill 1999; Giraudeau et al. 2014). Following prior work (Brawner et al. 2000; Surmacki and Hill 2014), coccidian oocyst number was estimated under a light microscope using a logarithmic scale (presence of no oocysts = a score of 0; 1–10 oocysts = 1; 11-100 oocysts = 2; 101-1000 oocysts = 3; 1001–10000 oocysts = 4; > 10000 oocysts = 5). Samples were prepared and scored at random by two observers (B.S. and E.H.) and identified only by individual band number to avoid observer bias.

Statistical Methods

All statistical analyses were conducted in the R statistical computing environment version 3.2.3 (R Core Team 2013), with an α value set to 0.05. Because the majority of variation in house finch plumage color can be assessed using hue, we focused on it here in our statistical analyses (Hill 2002; McGraw and Hill 2004). Moreover, we focused on rump patch size and hue (Figure 1) because the rump is the only body region in which both males and females consistently expressed carotenoid pigmentation and because rump hue explained a high degree of variation in mean hue for other color patches on the body (Appendix Table 1). Because not all female house finches have carotenoid coloration (in our study, 17 of the 45 females possessed some carotenoid pigmentation), we first tested whether urban and rural populations differed in the proportion of females having carotenoid-based rump coloration using logistic regression (with a binomial error term), setting color presence/absence as the response variable and urbanization as the predictor. Next, to understand determinants of plumage hue and ornament size, we ran analyses of variance (ANOVA), with urbanization, sex, coccidia score, body condition, and their interactions as predictors and either rump hue or rump patch size as the response. We performed post-hoc comparisons using Tukey’s honest significant difference (HSD) tests to compare the effects of urbanization on color for males and for females. To understand sex and site differences in parasite load, we used a generalized linear model (GLM) with quasipoisson error distribution to control for overdispersion, using urbanization, sex, body condition, and the urbanization*sex interaction as predictors and coccidia score as the response. In this analysis, the ‘sex’ variable included three levels: males, females with no carotenoid coloration (“non-ornamented”), and females with carotenoid coloration (“ornamented”), so we could detect differences in coccidia levels based on female color presence. We then used an ANOVA to test if body condition differed as a function of urbanization, sex, or their interaction.

Results

Urban birds are less colorful

As expected, females were less red and had smaller rump patches of color than males, and urban birds were less red than rural birds (Table 1). There was no effect of the urbanization*sex interaction on plumage hue in the full model ($F_{1,51} = 0.68, P = 0.41$), indicating that urbanization did not affect female hue differently than it did male
hue (Figure 2A). Urban birds of both sexes trended towards having smaller color patches than rural birds (Table 1, Figure 2B), but the urbanization*sex interaction again did not significantly affect rump patch area in the full model ($F_{1,51} = 1.07, P = 0.31$); therefore urbanization did not affect female patch size differently than it did male patch size (Figure 2B). Logistic regression showed a trend ($\chi^2 = 1.104, P = 0.08$) towards female finches from urban sites being less likely than rural females to possess any carotenoid-based plumage coloration (10 of 19 rural females had carotenoid color, compared to 7 of 26 urban females).

Sex-specific effects of urbanization on endoparasitism

We found no effect of urbanization on intensity of coccidial infection (Table 2). However, there was a significant effect of the urbanization*sex interaction on severity of coccidial infection, such that urban males had more severe coccidial infections than rural males (Table 2, Figure 3). However, post-hoc comparisons for ornamented females and for non-ornamented females showed that severity of coccidial infection did not differ significantly between rural and urban environments (Appendix Table 2). Also, among both rural female and urban female finches, ornamented females had similar levels of coccidial infection to non-ornamented females (Appendix Table 2).

Body condition in relation to sex, urbanization, and parasitism

We found no significant effects of sex, degree of urbanization, or their interaction on body condition (Table 1, Figure 4), allowing us to combine males and females for further analysis. There also was no significant relationship between body condition and intensity of coccidial infection (Table 2).

Relationship between plumage coloration and disease status differs for urban and rural birds

We found no significant effects of severity of coccidial infection or body condition on rump hue (Table 1). Coccidial infection severity also did not predict rump patch size (Table 1), and the relationship between rump hue and coccidial infection severity did not differ between rural and urban sites (Appendix Table 2). However, the coccidial infection severity*urbanization interaction did have a significant effect on plumage patch size (Table 1, Figure 5), such that among rural birds (as there was not a significant sex*site*coccidia interaction, $P > 0.05$) rump patch size decreased as coccidial levels increased; however, in urban birds, rump patch size increased as coccidial infection increased (rural regression: estimate = -35.11 ± 12.97, $t = -2.706, P = 0.010$; urban regression: estimate = 32.75 ± 8.62, $t = 3.80, P < 0.001$; Figure 5). Rump patch size also was significantly positively correlated with body condition regardless of sex or degree of urbanization (Table 1, Figure 6).

Discussion

Urbanization can decrease expression of carotenoid coloration in males of several avian species (Issakson et al. 2005; Jones et al. 2010), including house finches (Hasegawa et al. 2014; Giraudeau et al. 2015, 2018). Here, we
found that both males and females were less colorful in urban environments (Figure 2). Given strong selection pressures on male plumage color (Hill 2002; Giraudeau et al. 2018) and its previously demonstrated urban environmental sensitivity, we suspected that urbanization may affect rump color differentially between the sexes, but this was not the case. Urban-rural differences in carotenoid pigmentation have also been found in both sexes of great tit (Hõrak et al. 2001) and greenfinches (*Carduelis chloris*, Hõrak et al. 2004), suggesting that environmental variation affects the sexes similarly, and that male and female ornaments may be equally sensitive to city-related perturbations and pressures. Our results are consistent with these findings, though it is worth noting that urban impacts were not so strong as to override traditional sexual dichromatism in these species.

Disease prevalence among urban animals has been of great scientific interest, and it has been repeatedly demonstrated that city birds have higher rates of infection than their rural counterparts (Bradley et al. 2008; Delgado-Velez and French 2015), including in male house finches from our study populations during their molt period (Giraudeau et al. 2014). Here we detected a similar pattern to this for males just after molt, though surprisingly not for females, for which there was no effect of urbanization on coccidial scores (Figure 3). Intraseasonal sex differences in disease status have been reported previously in wild birds (e.g. Provencher et al. 2016), but we believe this to be one of the first reported instances where disease status in an urbanization context is sex-specific. Urban environments are thought to provide greater opportunity for social disease transmission via increases in density and contact of roosting and foraging birds (Zinke et al. 2004; Dolnik et al. 2010), though individual susceptibility may also differ owing to immunocompetence, stress, and other metrics of quality. Interestingly, Bonier et al. (2007) found sex-specific differences in corticosterone levels (CORT, a stress hormone) between urban and rural populations of white-crowned sparrows (*Zonotrichia leucophrys*), where urban males had higher CORT than their rural counterparts, but females did not. Thus, if stress reactivity or susceptibility differs between males and females in urban areas, this may have consequences for parasite burden (i.e., by investing in immune defenses differentially). There may also be differences in urban-specific foraging or social behavior that leads one sex to experience greater parasite/pathogen exposure; interestingly, in house finches, females are dominant to males at feeders (Belthoff and Gauthreaux 1991), which could leave males spending more time on these urban-abundant surfaces that transmit disease (Dhondt et al. 2007). We suggest that experimental studies will be key here for testing among these possible mechanisms underlying how cities differently impact parasitism in male and female finches.

We also examined the relationship between plumage color and disease in urban versus rural environments. We found that, although urbanization did not disrupt the previously demonstrated links between hue and infection (i.e. redder birds are less burdened by coccidial parasites), it did influence the relationship between patch size and parasite load (Table 1). Specifically, rural birds with large patches of color harbored fewer parasites – as predicted for condition-dependent color expression – but urban birds with large patches were more severely infected with coccidians (Figure 5). This reversal in honest-signaling association between colorful trait and health state begs the question - how might unhealthy birds in the city have improved their ability to express sexual ornamentation? Hutton and McGraw (2016) previously reviewed disruptions to honest signaling systems in urban environments, and argued that cities can shift the survival versus reproductive investments of animals. Sick animals facing worse prospects of survival, for example, may allocate energy into maximizing rapid/short-term reproductive investment (e.g. sexual signal production). Such a “terminal ornament investment” was
previously demonstrated in male three-spined sticklebacks (*Gasterosteus aculeatus*), which use red skin to signal breeding effort under conditions of extreme food deprivation (Candolin 1999). Alternatively, the degree of ornamentation may drive infection risk/intensity, such that, in urban areas where resources are scarce, more colorful females are less able to cope with infection. To date, we have not assessed how disease status or color expression are associated with age or fitness in our urban and rural finch populations, although we recently showed that female mate preferences in the different populations track the color appearance of the local birds (Giraudeau et al. 2018). Further work in this area may clarify the causes and values of such complex relationships between disease and ornamentation in this versatile songbird species that inhabits both natural and anthropogenically altered environments. It will also be useful to investigate the extent to which urban and rural finches differ in the developmental/genetic/pigment pathways underlying color production, especially considering the role of patch size here (Hill 1993c), and if expression of elaborate red color in urban birds has recently become dissociated from historically evolved (i.e. in natural habitats) parasite-mediated mechanisms.

We also considered relationships between body condition and sex, urbanization, parasitism, and ornamentation in this study, and found that, although finch body condition did not differ between the sexes, between urban and rural populations, or in relation to disease, it was positively correlated with extent of carotenoid-based plumage pigmentation (Figure 6). Prior work has shown that male finches in better nutritional condition grow redder feathers (Hill and Montgomerie 1994), and our results here on body condition per se are consistent with these findings. Production of these ornamental color patches is dependent on expending energy to obtain and process carotenoids (Hill 2000), thus making carotenoid coloration a condition-dependent trait in a wide range of taxa (Dufva and Allander 1996; Ibanez et al. 2006). Animals acquire these carotenoids through their diet, making foraging an important determinant of color expression (Senar and Escobar 2002; Hill et al. 2002), along with other factors that often relate to an individual’s body condition, such as stress levels (McGraw et al. 2011; Lendvai et al. 2013), metabolic rate (Kelly et al. 2012), and mitochondrial function (Hill et al. 2019). The fact that body condition was linked to coloration but not endoparasitism in our study suggests that there are separate mechanistic pathways underlying how these two common mediators shape ornamental color expression in finches.

In summary, females in our study populations of house finches express carotenoid-based traits that are sensitive to urbanization, as in males, but differed from males in the lack of effects of urban conditions on disease status. These findings underscore the need to consider both sexes in studies of environmental sensitivity and especially whether males and females from a variety of animal groups consistently respond differently to anthropogenic pressures. Although here we found that rural house finches were able to honestly signal their health (i.e. more ornamented birds had fewer parasites), the opposite was true for city birds, highlighting the need to comprehensively understand both the costs and complexities of signal expression (and its underlying mechanisms) under conditions of human-induced rapid environmental change.

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Figure 1. Photographs of house finches with patches of carotenoid color on their rump. We obtained both hue and patch size of each individual from their photograph. Examples of common rump coloration patterns are shown from left to right: red male (A), yellow/orange male (B), red female (C), and yellow female (D).
Figure 2. A) Effects of sex and capture site (i.e. urban v. rural) on rump hue in male and female house finches. Rump hue is in degrees (°), where a smaller numerical value indicates a redder hue and a higher value indicates a yellower hue. Urban birds are represented in black, rural birds are represented in gray, females are represented by the triangle shape, males are represented by the circle shape, and all points are mean hue ± SE. Unshared letters denote significant differences between groups. B) Differences in rump patch size (mm²) between male and female house finches from urban and rural sites. Urban birds are represented in black, rural birds are represented in gray, females are represented by the triangle shape, males are represented by the circle shape, and all points are mean patch size ± SE. Unshared letters denote significant differences between groups.
Figure 3. Violin plot illustrating coccidia scores for males and for females (showing non-ornamented and ornamented birds separately) from our urban and rural capture sites. The width of the shaded area shows the proportion of individuals out of those sampled with the corresponding y-axis coccidia score. We also note that the urbanization*sex interaction effect shown here is also significant when sex is modeled as simply male v. female (data not shown).
**Figure 4.** Violin plot showing body condition (i.e. the residuals from a mass/tarsus regression; see Methods for details) for males and for females (showing non-ornamented and ornamented birds separately) from our urban and rural capture sites. The width of the shaded area shows the proportion of individuals out of those sampled with the corresponding y-axis coccidia score.
Figure 5. Scatterplot illustrating the relationship between coccidia score and rump patch size (area in mm²). Urban birds are represented in black, rural birds represented in gray, females are represented by the triangle shape, and males are represented by the circle shape. Lines capture the trends for urban (in black) and rural (in gray) birds.
Figure 6. Scatterplot showing that birds with larger rump patches of carotenoid coloration were in better body condition.
Table 1. Analyses of variance (ANOVA) testing the effects of urbanization, sex, coccidia score, body condition (for color analyses only), and their interactions on plumage hue, patch size, and body condition. Non-significant interaction terms were omitted here. Degrees of freedom (abbreviated “df”) are listed as numerator, denominator. Significant predictors of the corresponding response variable are in bold.

| Response          | Predictor                      | Sums Squares | df     | F      | P       |
|-------------------|--------------------------------|--------------|--------|--------|---------|
| Rump Hue          | Coccidia Score                 | 18.70        | 1, 51  | 0.44   | 0.51    |
|                   | Urbanization                   | 377.70       | 1, 51  | 9.03   | 0.004   |
|                   | Body Condition                 | 0.100        | 1, 51  | 0.00   | 0.96    |
|                   | Sex                            | 2777.80      | 1, 51  | 66.42  | < 0.001 |
| Rump Patch Size   | Coccidia Score                 | 446.00       | 1, 51  | 0.04   | 0.83    |
|                   | Urbanization                   | 34434.00     | 1, 51  | 3.43   | 0.07    |
|                   | Body Condition                 | 79092.00     | 1, 51  | 7.88   | 0.007   |
|                   | Sex                            | 322886.00    | 1, 51  | 32.15  | < 0.001 |
|                   | Coccidia Score*Urbanization    | 73323.00     | 1, 51  | 7.30   | 0.009   |
| Body Condition    | Urbanization                   | 0.59         | 1, 89  | 3.01   | 0.49    |
|                   | Sex (3 levels)                 | 4.98         | 2, 89  | 28.20  | 0.13    |
|                   | Urbanization*Sex (3 levels)    | 6.64         | 2, 89  | 3.32   | 0.07    |
Table 2. Generalized linear model (with quasipoisson distribution to correct for overdispersion) testing for significant differences in coccidia score as a function of urbanization, sex, body condition, and interactions. Non-significant interaction terms were omitted, and significant predictors of coccidia score are in bold. Sex is separated into three levels: males, females with no carotenoid coloration (“non-ornamented”), and females with carotenoid coloration (“ornamented”), so we could detect differences in coccidia levels based on female color presence. “$t$” indicates the test statistic, i.e. how many standard deviations our estimate is from zero, and the direction of the relationship between the predictor and response. Pr > |$t$| is the probability of a difference being equal or larger than $t$ under the null hypothesis.

| Response       | Predictor            | Estimate ± SE | $t$    | Pr > |$t$| |
|----------------|----------------------|---------------|--------|------|---|
| Coccidia Score| Urbanization         | -0.49 ± 0.43  | -1.14  | 0.26 |
|                | Sex: Ornamented Females | 0.27 ± 0.40  | 0.65   | 0.51 |
|                | Sex: Males           | -0.67 ± 0.42  | -1.60  | 0.12 |
|                | Body Condition       | -0.07 ± 0.10  | -0.69  | 0.49 |
|                | Urbanization*Sex: Ornamented Females | -0.49 ± 0.71 | -0.69  | 0.50 |
|                | Urbanization* Sex: Males | 1.45 ± 0.53  | 2.71   | 0.008|
**Appendix Table 1.** Correlations between rump color metrics and whole-body (average of crown, breast, and rump) color metrics for both sexes of house finch ($n = 96$). $r$ is the correlation coefficient obtained from regressing variables against each other.

| Sex   | Whole body color variable | Rump color variable | $r$  |
|-------|---------------------------|---------------------|------|
| Male  | Hue                       | Rump hue            | 0.93 |
| Male  | Saturation                | Rump saturation     | 0.81 |
| Male  | Brightness                | Rump brightness     | 0.69 |
| Female| Hue                       | Rump hue            | 0.92 |
| Female| Saturation                | Rump saturation     | 0.77 |
| Female| Brightness                | Rump brightness     | 0.71 |
Appendix Table 2. Pairwise differences (95% confidence interval from post-hoc Tukey tests) in coccidia burden among different groups of finches, categorized by sex, extent of ornamentation in females, and capture site. “CC” denotes females with carotenoid coloration in their plumage (i.e. ornamented), whereas “NCC” denotes females with no carotenoid coloration (i.e. absence of ornamentation). Significant differences between groups are in bold.

| Comparison of differences in coccidia score                              | Ratio coccidia differences ± SE | z ratio | P    |
|------------------------------------------------------------------------|---------------------------------|---------|------|
| NCC rural females vs. NCC urban females                                | 1.82 ± 0.57                     | 1.92    | 0.39 |
| NCC rural females vs. CC rural females                                 | 0.78 ± 0.23                     | -0.82   | 0.96 |
| NCC rural females vs. CC urban females                                 | 2.11 ± 0.93                     | 1.69    | 0.54 |
| NCC rural females vs. rural males                                      | 2.20 ± 0.67                     | 2.58    | 0.10 |
| NCC rural females vs. urban males                                      | 0.79 ± 0.21                     | -0.89   | 0.95 |
| **NCC urban females vs. CC rural females**                             | **0.43 ± 0.12**                 | **-2.95** | **0.04** |
| NCC urban females vs. CC urban females                                 | 1.16 ± 0.50                     | 0.34    | 0.99 |
| NCC urban females vs. rural males                                      | 1.20 ± 0.35                     | 0.64    | 0.99 |
| **NCC urban females vs. urban males**                                  | **0.43 ± 0.11**                 | **-3.38** | **0.009** |
| CC rural females vs. CC urban females                                  | 2.70 ± 1.15                     | 2.34    | 0.18 |
| **CC rural females vs. rural males**                                   | **2.81 ± 0.78**                 | **3.72** | **0.003** |
| CC rural females vs. urban males                                       | 1.01 ± 0.23                     | 0.05    | 1.00 |
| CC urban females vs. rural males                                       | 1.04 ± 0.44                     | 0.09    | 1.00 |
| CC urban females vs. urban males                                       | 0.38 ± 0.15                     | -2.46   | 0.14 |
| **Rural males vs. urban males**                                        | **0.36 ± 0.09**                 | **-4.33** | **0.0002** |